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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Notes on Larvae, Juveniles, and Spawning of Bonito (*Sarda*) from the Eastern Pacific Ocean

W. L. KLAWE[1]

TWO SPECIES OF BONITO occur along the Pacific coast of the Americas (Hildebrand, 1946).[2] *Sarda chiliensis* ranges from southern British Columbia to northern Chile; the other species, *S. orientalis,* is found from Baja California to the Galapagos Islands and northern Peru. These species are of considerable importance to both commercial and sport fisheries of certain countries (Walford, 1937; Berdegué, 1956). The bonito fishery in Peru, especially for *S. chiliensis,* is particularly important. It contributes significantly to the economy, being valuable to the domestic market as well as for export. The following table gives the commercial catches of bonito, expressed in thousands of metric tons, during the past few years:

	OFF PERU	OFF CALIF.	WORLD TOTAL
1950	31.8	0.3	61.6
1951	51.2	0.4	76.9
1952	50.3	1.0	76.1
1953	44.4	1.4	83.8
1954	52.8	1.1	114.4
1955	71.8	0.1	173.1
1956	83.4	0.1	189.9
1957	58.6	0.1	145.5
1958	66.2	2.4	163.5

Despite the commercial importance of bonitos, knowledge of their biology is relatively meager. Little is known of the early life history and spawning, and descriptions of the eggs, larvae, and juveniles of *Sarda* are limited to a few reports. The only descriptions of young bonitos from the eastern Pacific Ocean are those of *S. chiliensis* by Barnhart (1927) and Orton (1953*a*, 1953*b*). Descriptions of eggs and young from other parts of the world seas are limited to the reports listed in Table 1.

The information on spawning of bonito is scant. According to Vildoso (1955), *S. chiliensis* reproduces in Peruvian coastal waters from October to March with the peak of spawning occurring from December to February. From Barnhart's work (1927) it is evident that off La Jolla, California, *S. chiliensis* spawns in June. Walford (1937) stated that in the northern latitudes this species spawns during the late spring and summer close to shore to as far out as 80 mi. Observations on spawning bonito in other parts of the world are limited to the reports on *S. sarda* tabulated below:

AREA	SPAWNING TIME	REFERENCE
Mediterranean	May–Jun.	Sanzo, 1932
Black Sea	Apr.–Aug.	Borcea, 1939, 1933 Vodyanitsky, 1936 Malyatsky, 1940 Numan, 1955
Atlantic,		
off Morocco	Jun.–Jul.	Furnestin *et al.*, 1958
off Dakar	Feb.–Mar.	Frade and Postel, 1955
U.S. coast	Jul.	Sette, 1943
	Jun.	Bigelow and Schroeder, 1953

During the course of collecting biological material and other scientific data from commercial fishing vessels and research ships operating in waters of the eastern Pacific Ocean, staff members of the South Pacific Fishery Investigations of the U. S. Bureau of Commercial Fisheries, Scripps Institution of Oceanography, and the Inter-American Tropical Tuna Commission have captured a variety of larval and juvenile fish, including young of *Sarda.* The data on the collections of young bonito made by these organizations with some other records, kindly put

[1] Inter-American Tropical Tuna Commission, La Jolla, California. Manuscript received September 26, 1960.

[2] It is assumed that *S. lineolata* (Girard) = *S. chiliensis* (Cuvier and Valenciennes) and that *S. velox* Meek and Hildebrand = *S. orientalis* (Temminck and Schlegel). *S. chiliensis* and *S. sarda* from the Atlantic Ocean and adjacent seas may be synonymous. A detailed discussion on the relationship of the species of the genus *Sarda* is provided by Godsil (1955).

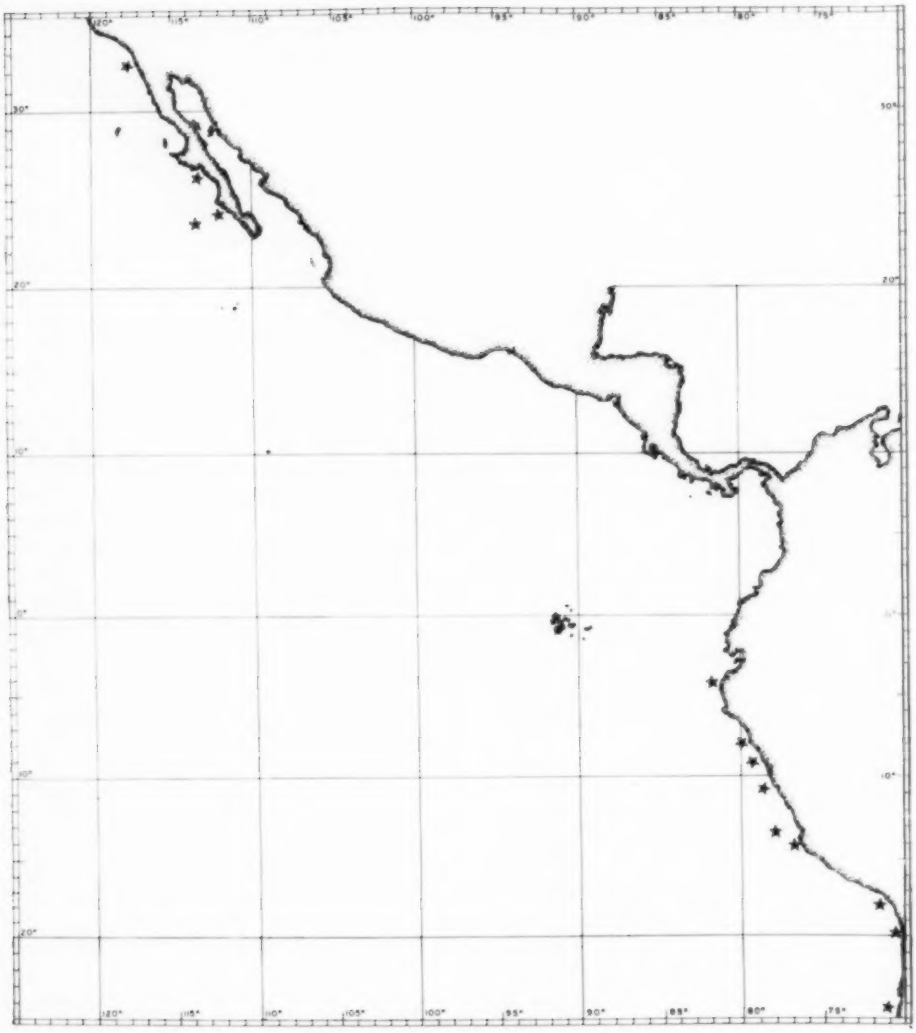

FIG. 1. Localities of capture of young *Sarda* in eastern Pacific Ocean.

at the Commission's disposal, are given in Table 2. The geographical distribution of these catches is shown in Figure 1.

The author wishes to thank Mr. Gerald V. Howard and Dr. Elbert H. Ahlstrom of the U. S. Bureau of Commercial Fisheries for their helpful criticism and suggestions on the preparation of this manuscript. The manuscript upon its completion in 1959 was made available to Mr. Leo Pinkas of the California Department of Fish and Game. Thanks are extended to Sra. Aurora Chirinos de Vildoso of the Peruvian Pesca y Caza for her cooperation in exchange of various data.

TABLE 1

SPECIES	MONTH COLLECTED	PLACE	SIZE OR STAGE	REFERENCE
S. sarda	Jun.	Mediterranean	7.2 mm.	Ehrenbaum, 1924
S. sarda	Jul.	Mediterranean	26.5, 32 mm.*	de Buen, 1930
S. sarda	Jun.	Mediterranean	eggs and early larvae	Sanzo, 1932
S. sarda	Jun.	Black Sea	eggs and early larvae	Vodyanitsky, 1936
S. sarda	Mar.	Gulf of Mexico	64, 67 mm.	Klawe and Shimada, 1959
S. sarda	Feb.	Western Atlantic	34 mm.	Klawe, in press
S. orientalis	Apr.	Japan	170 mm.	Kishinouye, 1923
S. orientalis	Sep.	Japan	230 mm.	Kishinouye, 1923

* The 17.5 mm. individual represented by de Buen (1930) in figure 1 and originally identified by him as *Sarda sarda* has 39 vertebrae and was reidentified by him as *Auxis thazard* (de Buen, 1932).

DESCRIPTION AND IDENTIFICATION OF LARVAE AND JUVENILES

Two larvae of total lengths 2.9 and 3.5 mm. captured in a plankton tow off Baja California (Table 2) have been previously identified as those of *Sarda* by Alhstrom. An illustration of the larger specimen is given in Figure 2. These larvae have the usual characteristics of larval scombroid fishes. When the material was compared with Sanzo's (1932) and Vodyanitsky's (1936) descriptions and illustrations of larvae of *S. sarda* hatched in the laboratory, the similarity was obvious, although their specimens were less advanced in development. Sanzo and Vodyanitsky report that their lavae measured about 4.3 mm. However, Sanzo and Vodyanitsky were working with fresh material, while the planktonic larvae caught off Baja California had been preserved in formalin.

Barnhart's (1927) observations concerning larval bonito are based on material hatched in the laboratory from eggs collected in a plankton net off La Jolla, California. One of the striking differences between his description and that of *S. sarda* by Sanzo and Vodyanitsky and that of *S. chiliensis* by Orton (1953*a*, 1953*b*) is the absence of melanophores in Barnhart's material. Barnhart credits the newly hatched bonito with a few yellow chromatophores; on the other hand, Sanzo and Vodyanitsky show that in addition to the yellow pigment there are melanophores on the eggs just prior to hatching and the larvae are also provided with numerous melanophores. Barnhart based his description upon material which probably had been preserved in Bouin's solution, which has the property of fading melanine according to Orton (1955).

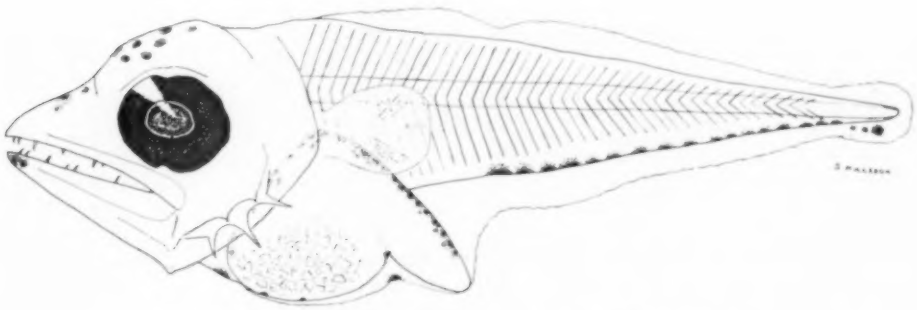

FIG. 2. A 3.5 mm. *Sarda* sp. caught on August 12, 1951, off Baja California.

TABLE 2

RECORDS OF CAPTURE OF DEVELOPING EGGS AND YOUNG *Sarda* FROM THE EASTERN PACIFIC OCEAN

DATE	GENERAL LOCALITY	LATITUDE	LONGITUDE	HOW CAPTURED	SIZE,[1] mm.	NO.	SPECIES	REFERENCE OR COLLECTOR
Jun. 30, 1927	off La Jolla, Calif.			plankton net	eggs	?	*chiliensis*	Barnhart, 1927
May 17–18, 1947	off La Jolla, Calif.			night light, dip net	post-larva	1	*chiliensis*	Hubbs[2]
Feb. 20, 1951	off Pt. Lobos, Peru			?	125–130	3	*chiliensis*	Vildoso, 1955
Aug. 5, 1951	off Baja Calif., Mexico	25° 35′ N.	113° 56′ W.	night light, dip net	42	1	*chiliensis*	Fish & Wildlife Service[3]
Aug. 12, 1951	off Ballenas Bay, Baja Calif., Mexico	26° 29.5′ N.	113° 29.2′ W.	plankton net	2.9, 3.5	2	?	Fish & Wildlife Service[3]
Jan. 3, 1956	off Pt. Negra, Peru			bait net	143–164	3	*chiliensis*	M.V. "Corsair"[4]
Dec. 10, 1957	Independencia Bay, Peru	14° 14′ S.	76° 12′ W.	bait net	128	1	*chiliensis*	B.M. Chatwin & P. Boylan[4]
Dec. 18, 1957	off Ilo, Peru			bait net	70–135	3	*chiliensis*	Arnold Neves[5]
Dec. 31, 1957	off Pt. Pichalo, Chile	19° 35′ S.	70° 16′ W.	night light, dip net	37	1	*chiliensis*	B.M. Chatwin & P. Boylan[4]
Jan. 3, 1958	off Pt. Dos Reyes, Chile	24° 30′ S.	70° 49′ W.	night light, dip net	39	1	*chiliensis*	E. Brinton[5]
Jan. 3, 1958	off Pt. Dos Reyes, Chile	24° 36′ S.	71° 01′ W.	night light, dip net	36–44	3	*chiliensis*	E. Brinton[5]
Jan. 14, 1958	SW off Fraile Pt., Peru	13° 14.8′ S.	77° 55.5′ W.	night light, dip net	34	1	*chiliensis*	E. Brinton[5]
Feb. 1958	off Chimbote, Peru			bait net	89–129	3	*chiliensis*	Arnold Neves[5]
May 6, 1958	Almejas Bay, Baja Calif., Mexico			bait net	103	1	*chiliensis*	M.V. "Lou Jean"[4]
Feb. 1, 1959	Sama Cove, Peru			bait net	111	1	*chiliensis*	M.V. "Normandie"[4]
Mar. 15, 1959	off Ilo, Peru			?	135–160	3	*chiliensis*	P. Talledo[6]
Mar. 16, 1959	off Barranca, Peru			?	173, 199	2	*chiliensis*	Vildoso[6]

[1] Direct distance from tip of snout to tip of shortest median caudal ray.
[2] Field-book data of C. L. Hubbs, Scripps Institution of Oceanography, La Jolla, Calif.
[3] In the collection of the South Pacific Fishery Investigations of the U.S. Fish and Wildlife Service, La Jolla, Calif.
[4] In the collection of the Inter-American Tropical Tuna Commission, La Jolla, Calif.
[5] In the collection of the Scripps Institution of Oceanography, La Jolla, Calif.
[6] In the collection of the laboratory of Pesca y Caza, Lima, Peru.

The planktonic specimens caught off Baja California have between 43 and 45 myomeres, the actual number being difficult to establish. The mouth is large and contains a set of large teeth. There are three spines along the posterior edge of the preoperculum. The unpaired fins show little development and are still represented by the median fin fold. The embryonic pectorals can be distinguished but there is no indication of the pelvics. The pigmentation of the head consists of distinct chromatophores over the area of the brain and an aggregation of what appears to be a group of chromatophores at the symphysis of the pectoral girdle. There

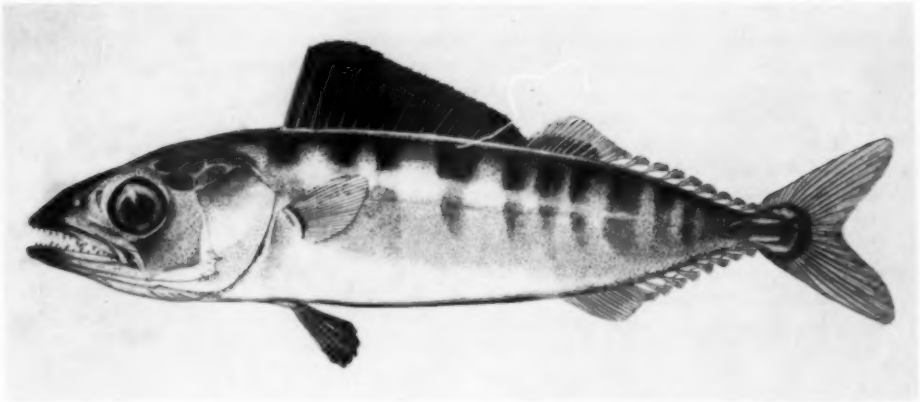

FIG. 3. A 42 mm. *Sarda chiliensis* caught on August 5, 1951, off Baja, California. Drawing by George Mattson of the U. S. Bureau of Commercial Fisheries.

are concentrations of chromatophores in various parts of the peritoneum but especially along its dorsal portion. A series of chromatophores can also be seen along the mid-ventral line extending almost to the tip of the urostyle.

Identification of the two specimens, as to which of the two species they represent (*S. chiliensis* or *S. orientalis*), is impossible without a complete developmental series.

Other specimens of *Sarda* available from the eastern Pacific Ocean are several individuals over 30 mm. in length caught off Chile and Peru and two individuals caught off Baja California. On the basis of gill raker counts (see next paragraph), all individuals have been identified as *S. chiliensis*. A 43 mm. individual caught off Baja California is illustrated in Figure 3. The general appearance of these juveniles resembles that of *Euthynnus* sp. However, separation between these fishes is possible, as the outline of the first dorsal fin is concave in *Euthynnus* and convex in *Sarda* when the spines are erect. Upon closer examination the two genera can be separated easily, as the meristic counts differ considerably. The densely pigmented pelvic fins shown in Figure 3 are characteristic of small *Sarda*. It is worthwhile to mention that the first dorsal fin in small *S.*

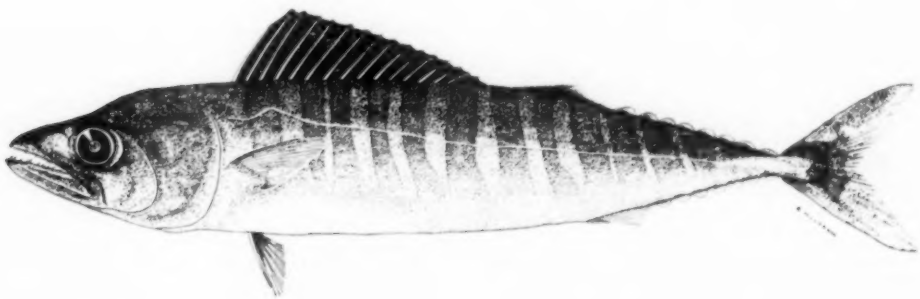

FIG. 4. A 160 mm. *Sarda chiliensis* caught on January 3, 1956, off northern Peru.

chiliensis is either dark with a lighter area in the posterior region of that fin or is uniformly dark. The bodies of all juvenile *S. chiliensis* examined are striped vertically. This also applies to other species of *Sarda* (Kishinouye, 1923; de Buen, 1930; Furnestin *et al.*, 1958; Klawe and Shimada, 1959). A 160 mm. individual of *S. chiliensis* is illustrated in Figure 4. The vertical striations still persist. According to Vildoso (1955), these vertical bars are replaced by oblique markings characteristic of *S. chiliensis* at an approximate length of 320 mm. It should be mentioned that adult *Sarda chiliensis*, when captured, briefly exhibit dusky vertical bands quite like those on preserved juveniles, although not as intense. The body shape of the specimen illustrated in Figure 4 is like that of an adult. The pigmentation of the pelvic fins at this size is confined only to the more basal portion.

As the gill rakers are one of the characteristics used for separating adults of *S. chiliensis* from *S. orientalis*, it is important to establish at what length they develop and at what length the final complement is attained. The gill raker counts for adult fish are 7 to 10 + 12 to 19 for *S. chiliensis*[3] and 2 to 3 + 6 to 10 for *S. orientalis*. Some idea can be obtained from the following counts made on several smaller *S. chiliensis* caught off Peru and Chile.

SIZE, mm.	NO. OF GILL RAKERS	SIZE, mm.	NO. OF GILL RAKERS
34	7+1+15	89	7+1+17
36	7+1+15	94	9+1+16
37	4+1+16	106	7+1+15
39	5+1+14	111	8+1+17
41	7+1+15	128	9+1+17
44	7+1+16	129	7+1+15
70	7+1+18	135	7+1+15

CONCLUSIONS

All evidence indicates that spawning of *S. chiliensis* takes place in the warmer season off California, Baja California, Peru, and northern Chile. It appears that it should be possible to distinguish between juveniles of *S. chiliensis* and *S. orientalis* by means of gill raker counts even at a relatively small size.

[3] Author examined 25 specimens of *S. chiliensis* caught off San Diego, California, on September 22, 1959, ranging in length from 330 mm. to 380 mm. The gill raker counts for this group of fish were 7 to 9+1+15 to 18.

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The Distribution of Certain Benthonic Algae in Queen Charlotte Strait, British Columbia, in Relation to Some Environmental Factors

ROBERT F. SCAGEL[1]

IN COMPARISON with the progress in our knowledge of most groups of plants—especially concerning their life histories and distributions—the advances made in marine phycology and marine ecology have been relatively slow. The limited access to living material or to the facilities to maintain the larger marine algae in the living condition for a prolonged period of time, the difficulties of collection—particularly in the subtidal zone—and the lack of any extensive direct economic importance until recent years have all contributed to this slow progress. However, in spite of these difficulties there has been a considerable amount of interest in the marine algae, including a number of studies of their ecology. Although this interest has been fairly widespread in a number of countries, until recently there has been little activity in the field of marine ecology relating to the benthonic algae on the Pacific Coast of North America and nothing of a comprehensive nature has been published for this area. It is an anachronism that this should be so in a region which received such prominence some 50 years ago through the efforts of a pioneer in the field, the late William Albert Setchell (1893, 1917, 1935).

Knowledge of the effect of temperature on the world-wide distribution of plants both horizontally and vertically had developed gradually over a period of many years. However, it was only during the last hundred years that the attention of phycologists was brought to a consideration of the reasons for the observed distributions of the marine algae. The historical development of this trend of thought and investigation has been reviewed by Setchell (1917). Starting over 50 years ago, through a series of papers from 1893 to 1935, Setchell made a noteworthy attempt to explain the world-wide distribution of marine algae, especially of members of the Laminariales on the Pacific Coast of North America, on the basis of latitudinal and seasonal temperature distributions. The physical data available during this early period were limited, but many of the principles set forth by Setchell concerning the distributions of marine algae are as sound now as when they were first proposed. Except for more precise knowledge of the physical and chemical factors of the environment and the distributions of the algae concerned, much of Setchell's ecological work can still be used as a good foundation for further study. Although it was largely a two-dimensional approach to the marine environment, Setchell's work made a significant contribution to the development of marine algal ecology.

Lamouroux (1825, 1826) had suggested the possibility that temperature stratification in the sea might account for the vertical distribution of the marine algae and had considered the effect of tides on intertidal zonations, but this trend to analyze the vertical distribution of the marine algae was not generally taken up in detail until much later. Coleman (1933) was one of the first to emphasize the use of tide levels to account for the vertical distribution of the marine algae in the intertidal zone. In a study in Oregon, on the Pacific Coast of the United States, Doty (1946) has given further evidence for the relationship between the vertical distributions of marine algae and critical tide levels.

A number of lists of marine algae have been published and attempts have been made not only to relate the floras of one area to another, such as that by Okamura (1926, 1932) in the North Pacific, but also to account in a general way for distributions on the basis of ocean currents, such as that by Isaac (1935) in the area around South Africa and by Tokida (1954) in the region of northern Japan. However, there soon followed a decided shift to intertidal studies of regional areas, such as that by Feldmann (1937) in the Mediterranean and Chapman

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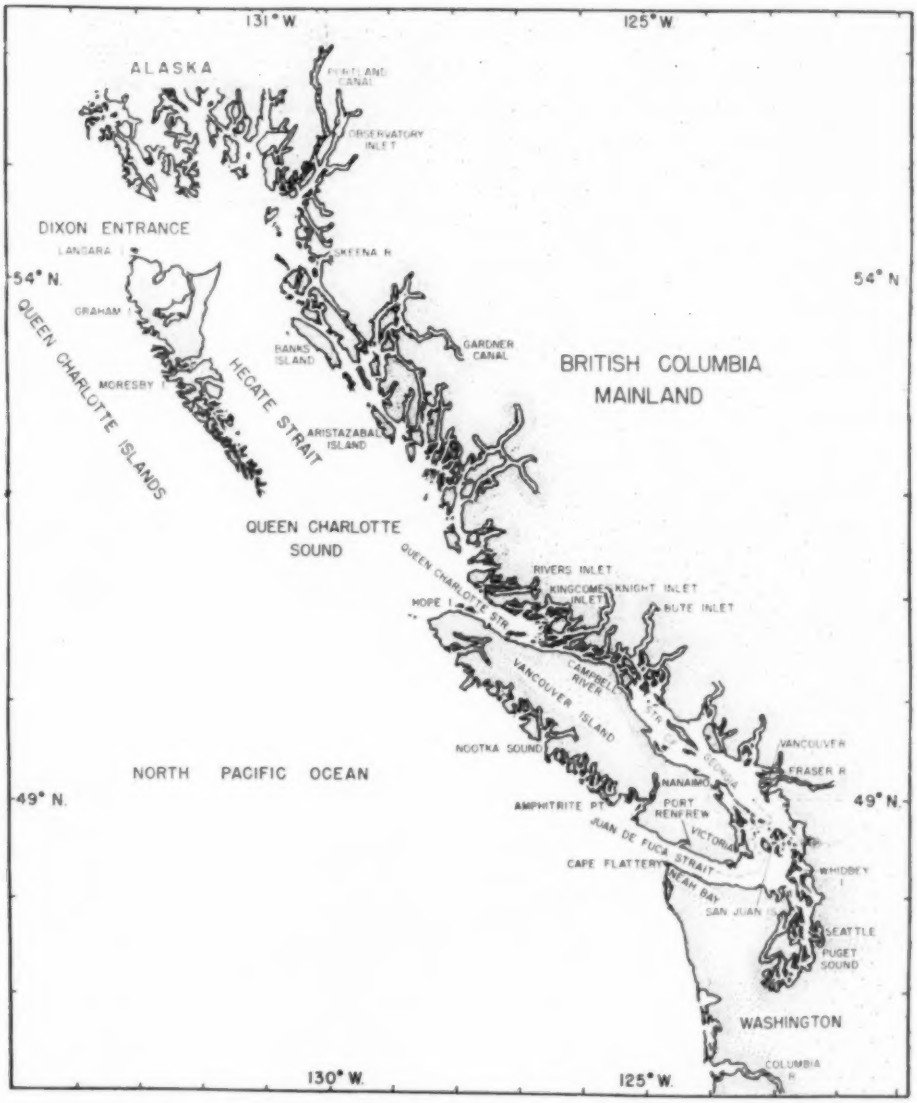

FIG. 1. Map of geographical features of the coast of British Columbia.

(1950) and his students in New Zealand. Some attempts have also been made to describe universal features of intertidal zonation throughout the world (Stephenson and Stephenson, 1949). At the same time there has been a tendency to place greater emphasis on the interrelationships between the various organisms.

Many of these intertidal studies have been of great value as an initial descriptive stage of investigation, and there is a need for further descriptive studies of this type in new and undescribed regions. However, the variety of systems of nomenclature and terms that have been proposed by marine ecologists to describe zonation, associations, and other ecological concepts has frequently only complicated the descriptive study rather than succeeded in explaining the observed phenomena. This has led to some confusion in terminology. It is a debatable point whether there can be such a thing as a universal system of classification beyond a generalized scheme, such as that proposed by Ekman (1935), and it is questionable whether some of the systems proposed can contribute further to progress in marine algal ecology even in regional studies without simplification or clarification. There have been a number of recent comprehensive papers dealing with various aspects of marine ecology which make it unnecessary to dwell at length on a review of the trends that have been followed more recently in marine algal ecology and the results that have been attained (Gislén, 1929, 1930; Feldmann, 1937, 1951; Fischer-Piette, 1940; Chapman, 1946, 1957; Doty, 1957; Hartog, 1959).

Although the shift in emphasis to the interrelationship of organisms was an important one, in some instances this approach has been responsible for excluding adequate concurrent studies of the physical and chemical aspects of the environment. It is for this reason that a case may be made for reassessing the status of marine algal ecology, and a critical evaluation of the steps to be taken to further its progress is timely. Perhaps what may be called a three-dimensional or an oceanographic approach can be used to analyze more precisely various factors in the marine environment and the relationship of these factors to the benthonic algae. Steps in this direction have been made more recently

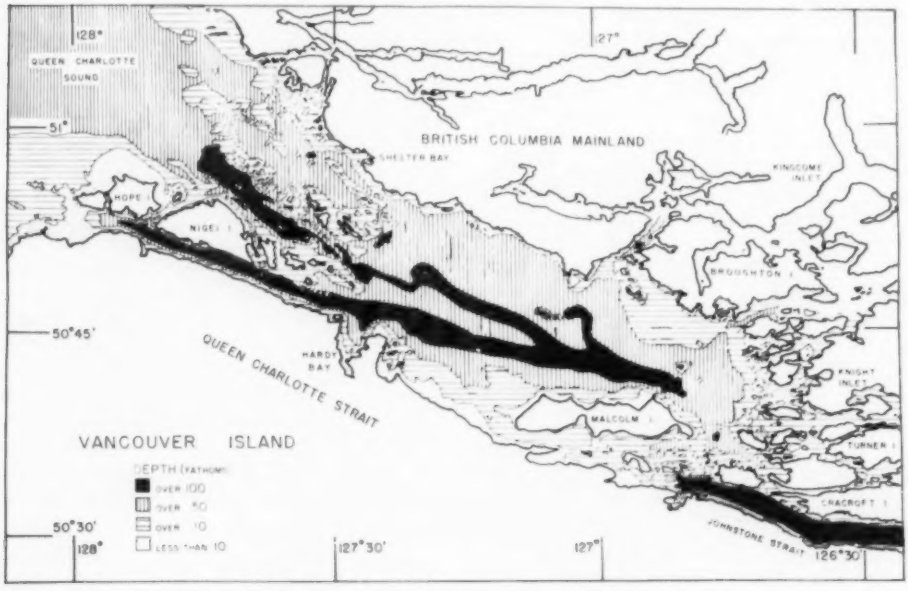

FIG. 2. Map of Queen Charlotte Strait showing depth contours.

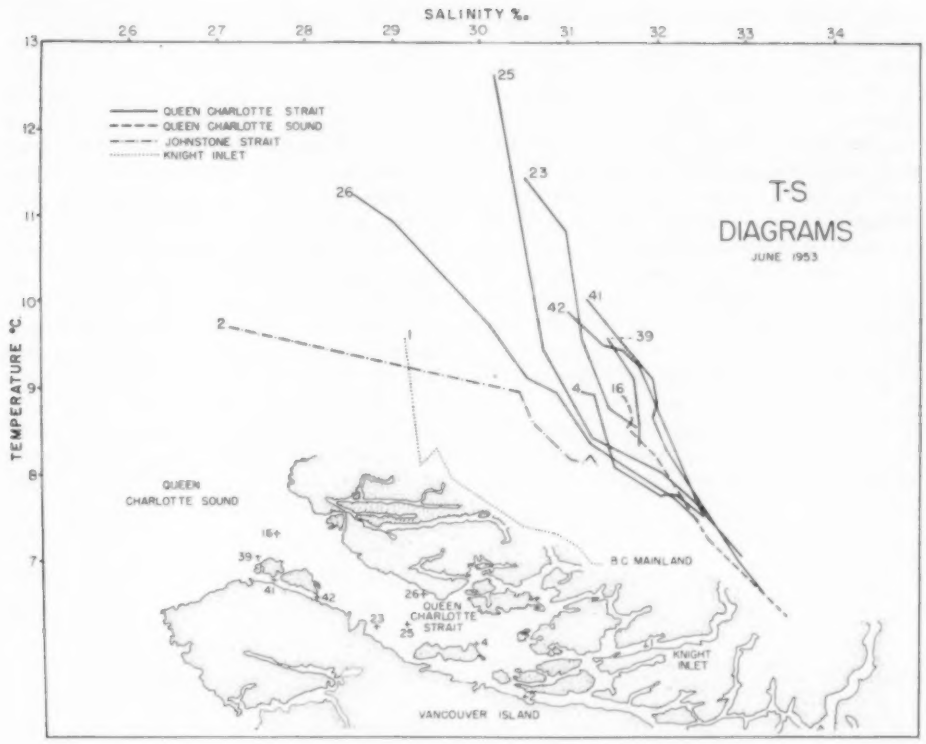

FIG. 3. T–S diagrams for stations in Queen Charlotte Strait and adjacent areas in June, 1953.

with some measure of success by Dawson (1945, 1951) in Baja California, Doty (1946) in Oregon, and Womersley (1956) in Australia.

The physical environment of the sea imposes problems of considerable magnitude which, in contrast to many land environments, presents formidable obstacles such as complex tidal and circulation patterns. In an effort to manipulate or simulate some aspects of this environment, both in the field as well as in the laboratory, the more generally available resources are soon taxed. Thus the methods that have been used in marine algal ecology have, in many instances of necessity, been crudely quantitative, less than ideal experimentally, frequently encumbered by terminology as a result of limited concurrent physical and chemical data, and sometimes they have failed to establish clearly the objectives being sought. As a result most of the efforts in marine algal ecology have been descriptive rather than functional in nature. As in most oceanographic work there is value in an approach from the grosser aspects to the particular. To the oceanographer the most complicated physical or chemical situation to explain may be the smallest unit of the environment with which he is faced. This is partly a problem of instrumentation. However, it is usually much easier to recognize significant discontinuities in properties, such as temperature, salinity, and even plankton distributions, over extensive areas of the ocean than in restricted or local regions. It is also easier to use such information in describing dynamic processes. Hence, it is suggested that more attention should be given to studies of the general distribution of various physical and chemical properties in the marine environment in an attempt to set up some workable hypo-

theses to account for observed distributions of marine algae. In this way we may hope to explain and account for biological phenomena rather than be satisfied by a description of the phenomena or by devising terms to describe them which do nothing more than give names to dynamic aspects of marine ecology much in need of logical explanation. With the recent increased activity in oceanography in the Pacific we may now hope for more abundant and usable data on some of the more general oceanographic properties of the North Pacific. In specific cases, particularly in more restricted areas, the ecologist will be forced to turn more attention to obtaining *in situ* physical and chemical data before further progress can be made.

One can arbitrarily start by summarizing all the factors in the marine environment as geological, physical, chemical, and biological. The way in which these are considered may be somewhat a matter of interpretation. Salinity, for example, may be considered directly, from a chemical standpoint, or indirectly as a physical factor responsible for changes in density and thus contributing to the pattern of circulation. Likewise, the nature of the substratum may be considered indirectly as a geological factor or directly as a physical or mechanical factor restricting or permitting establishment of benthonic organisms because of particle size. There has been much written on some of these aspects of ecological study in special cases, but it is suggested that, in a general over-all reassessment of the environment, an attempt be made to proceed from this more general position to the particular. This approach may initially lead only to the erection of further hypotheses, since the indirect or direct nature of the action of

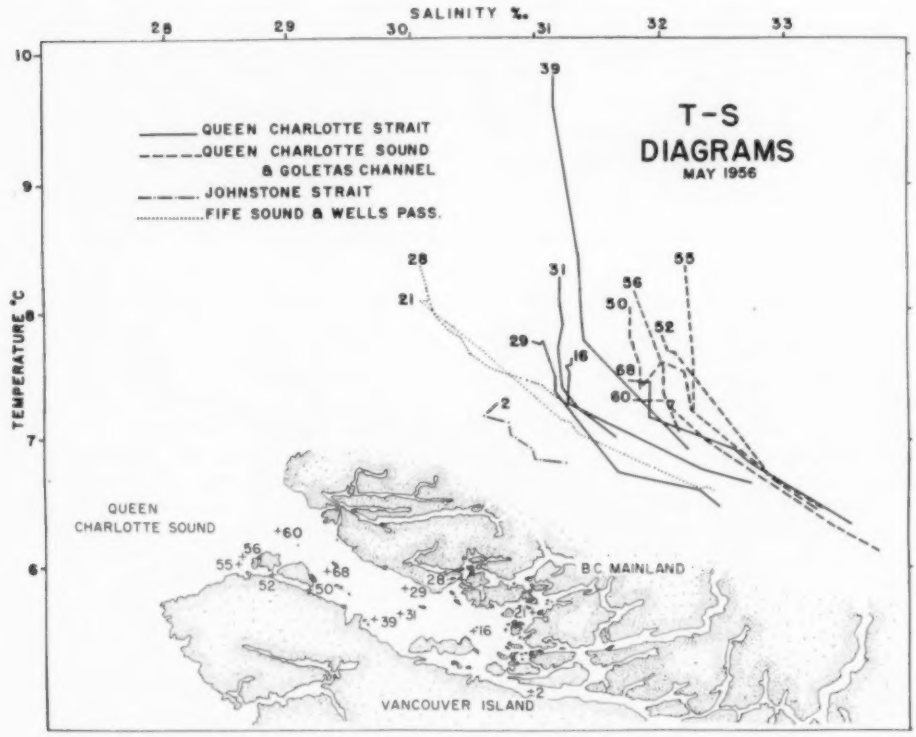

FIG. 4. T–S diagrams for stations in Queen Charlotte Strait and adjacent areas in May, 1956.

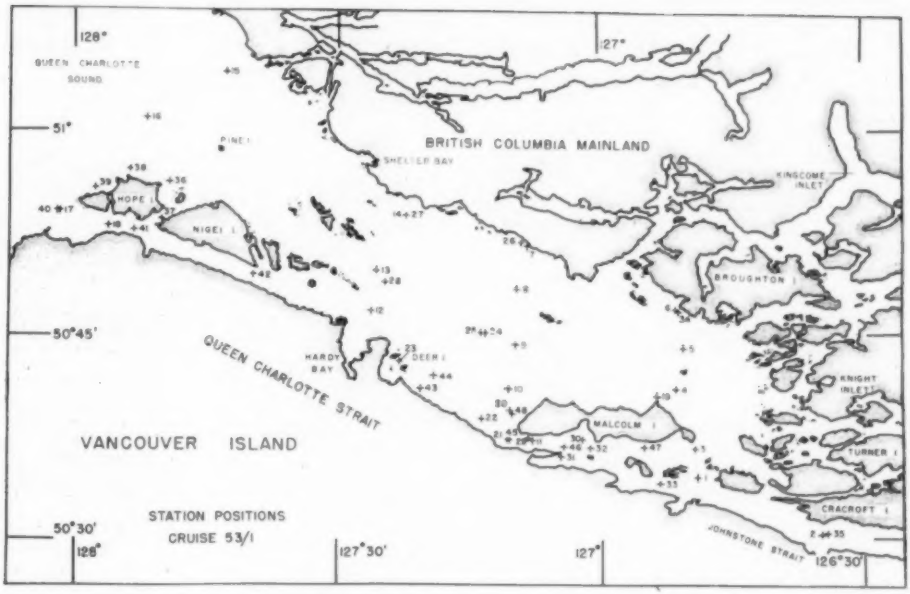

FIG. 5. Map of station positions in Queen Charlotte Strait in June, 1953.

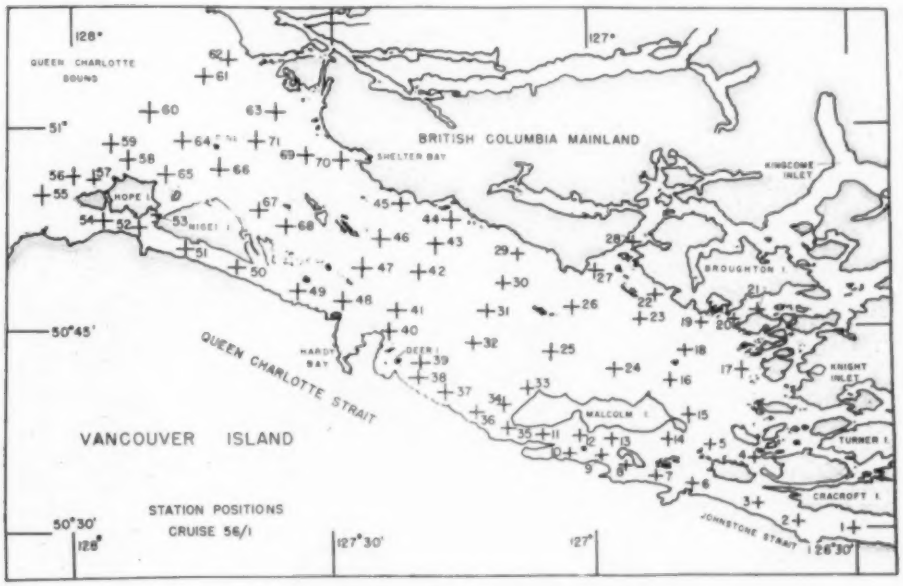

FIG. 6. Map of station positions in Queen Charlotte Strait in May, 1956.

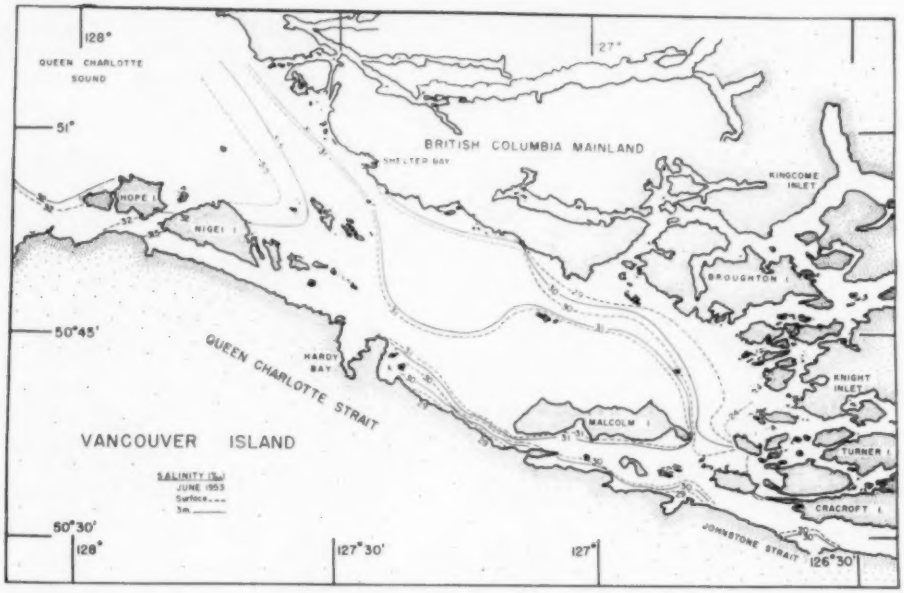

FIG. 7. Salinity distribution in Queen Charlotte Strait in June, 1953, at the surface and at a depth of 3 m.

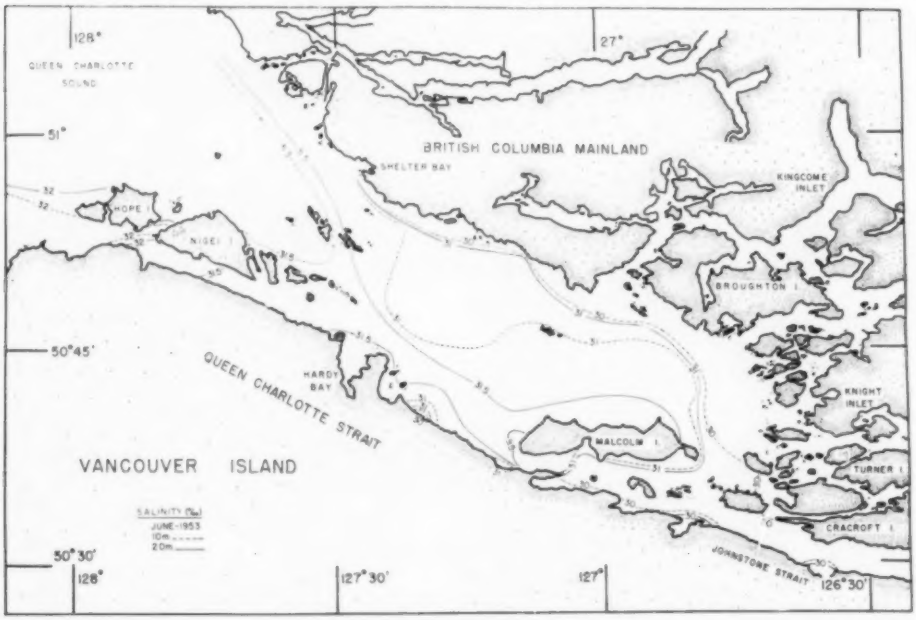

FIG. 8. Salinity distribution in Queen Charlotte Strait in June, 1953, at depths of 10 and 20 m.

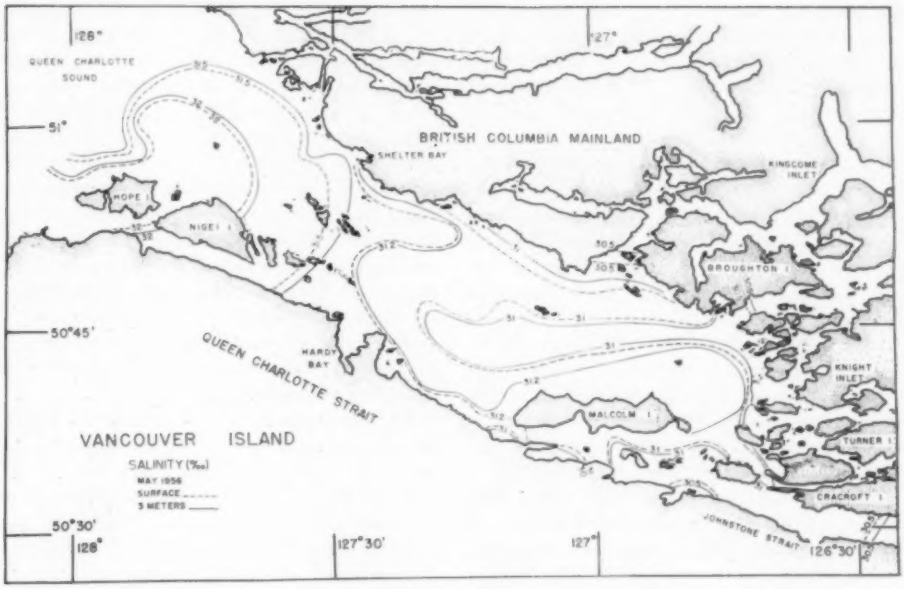

FIG. 9. Salinity distribution in Queen Charlotte Strait in May, 1956, at the surface and at a depth of 3 m.

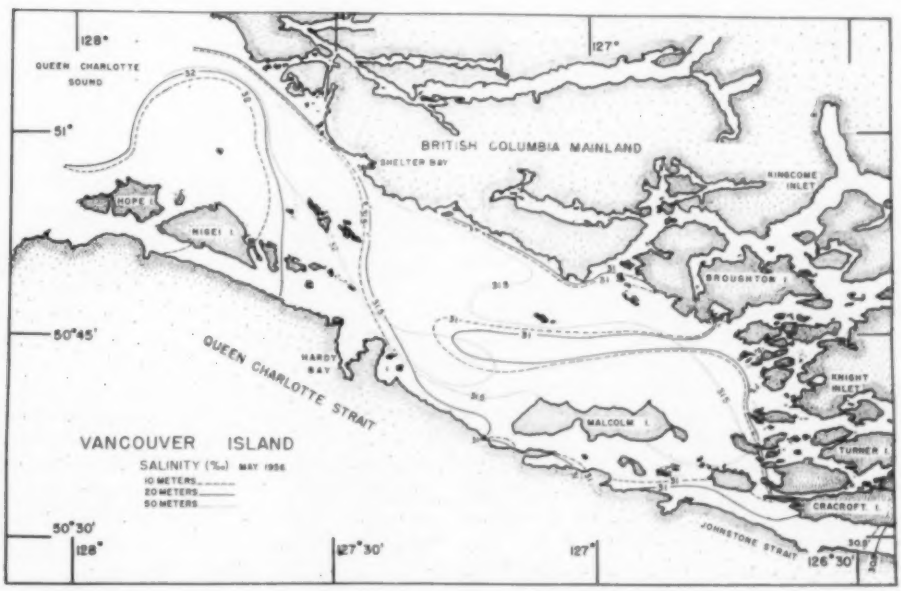

FIG. 10. Salinity distribution in Queen Charlotte Strait in May, 1956, at depths of 10, 20, and 50 m.

any particular factor in the environment may ultimately be established only by experimental work either in the field or in the laboratory. In some regions where the algal flora is well known taxonomically the descriptive aspect can and has been undertaken and the time has come when further progress in such an area can only be expected by undertaking experimental field and laboratory studies. In some regions, even where the flora may be well known, inadequate physical and chemical data militate against further progress and even the advancement of tenable hypotheses. Only when such hypotheses are put forward, based on a correlation of the observational data, can one anticipate and justify embarking on an experimental field and laboratory approach in an attempt to solve problems relative to the distribution of marine algae.

This is the approach that is outlined here in studies on marine organisms and, particularly on the marine algae, being carried out on the coast of British Columbia, some aspects of which will be considered here in detail. As a step in the direction of increasing our knowledge of the entities which comprise the tools of the algal ecologist and of completing this descriptive phase of the study of the marine benthonic algae, an annotated check list has been completed for the coast of British Columbia and northern Washington (Scagel, 1957). Based on this list, further studies are now in progress to augment the existing data on the marine flora of British Columbia, not only on distributions but also on life histories, growth, reproduction, and seasonal aspects. These fundamental studies are basic to all other aspects of ecological research, especially when an attempt is made to use specific organisms as indicators of oceanographic conditions.

Not only does this descriptive phase require an adequate consideration of the taxonomic aspects, but also a complete description of the other factors in the environment is needed. With increased activity recently and currently in general oceanographic studies of the North Pacific by a number of organizations on the Pacific

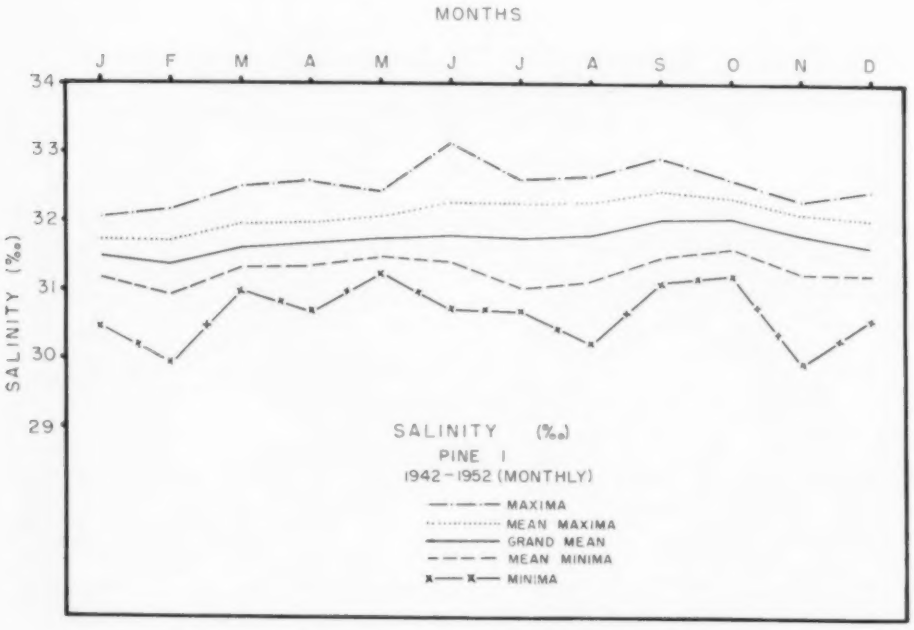

FIG. 11. Monthly salinities at Pine Island for the period 1942–52.

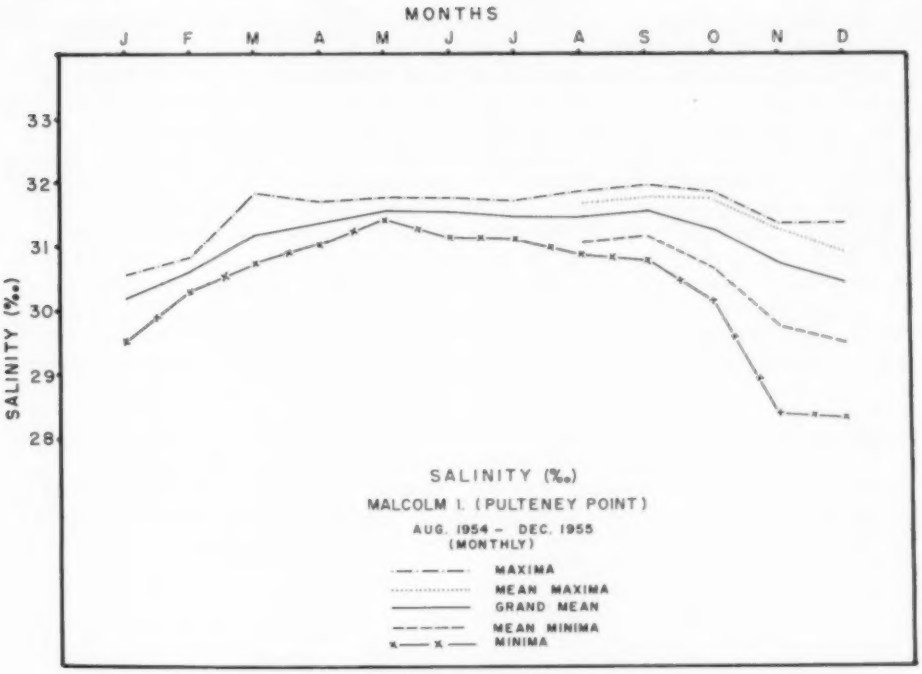

FIG. 12. Monthly salinities at Pulteney Point, Malcolm Island, for the period 1954–55.

Coast of Canada, in Japan, and in the United States, there has resulted a considerable body of scientific knowledge but it is still far from adequate for the ecologist, particularly for one interested in coastal dynamics. Circulation patterns, temperature, salinity, oxygen, and in some areas phosphate, silicate, and nitrate distributions are fairly well known in a broad and general sense, but at the present time these oceanographic data are known in sufficient detail for few restricted areas. Knowledge of the distribution of other chemical constituents and to a large extent even of the plankton composition, distribution, and activity is almost completely lacking. Much more information is needed in order to tackle many problems relating to specific distributions and to set up field and laboratory studies to test hypotheses.

It is already apparent that much can be done experimentally both in the field and in the laboratory with the benthonic algae. Many of the problems encountered by the ecologist dealing with large marine algae present unique culture problems both in the field as well as in the laboratory. Some studies of growth and reproduction, particularly of some of the larger Laminariales, have been done in this region both in the field (Scagel, 1948) as well as in the laboratory. Although the size of many of the cold-water marine algae adds special problems, at least some of the stages can be carried out to the point where transplant experiments can be made from the laboratory into the sea for further study. Transplant experiments of natural populations of juvenile stages, at least of these larger marine algae, even in the case of *Macrocystis*, are quite feasible.

The successful use of the experimental approach in the laboratory is primarily dependent on having facilities for maintaining temperature and light control, although the size of plants may again present certain special problems. Cultures of Laminariales have been maintained in controlled-environment tanks at the

University of British Columbia for as long as a year, during which the complete sexual generations were grown and the young sporophytes reached a length of 14 in., well past the stage where secondary morphological characteristics had developed to a point permitting positive identification. These studies have permitted indisputable identification of the sporophytes to genus, and in some cases to species. The study of cultures in this group suggests that much of the early work on gametophytes in the Laminariales and in fact even on the early sporophytes may be in some question. In most of the early studies reported in the literature, plants were not grown long enough to establish beyond doubt the characteristic secondary morphological features of the sporophytes of the genera from which zoospores were intially obtained. In the presence of contaminating zoospores of other species which can soon supplant the original species under study, there is no other way of establishing that the same species or even the same genus in the Laminariales was obtained in the sporophyte generation succeeding the gametophyte generations in culture.

It would be remiss not to mention much of the worthwhile physiological work that has been done on marine algae and other organisms. However, there is a need for a great deal more physiological work, particularly of the type done by Gail (1918, 1919, 1922) in an attempt to relate physiological processes more specifically and directly to the environment and ecological problems encountered in the field. In physiological studies there is frequently a tendency to proceed more and more deeply into special aspects of the physiological behaviour or the biochemistry of an organism under artificial conditions. Although this information is very often of great value there is a very real need to project back to the field and attempt to explain behaviour under the conditions existing in the natural environment. The statistical approach, as illustrated by Berquist's (1959) revealing study of *Hormosira*, has also been little used as yet.

Almost all of the quantitative aspects of the productivity of the benthonic algae in this area have related to species of economic interest (anon., 1947, 1948*a*; Scagel, 1948; Hutchinson, 1949). These studies have dealt largely with harvestable quantities and distributions, and have contributed little to an evaluation or an explanation, in terms of oceanographic factors, of the causes for this production.

Obviously the ideal of a functional interpretation in the ecology of marine benthonic algae is dependent on an adequate and balanced knowledge of all of the foregoing aspects—of the qualitative and quantitative features of both the organisms and the environment. Many, much needed data are still lacking. An attempt to follow this line of investigation has been pursued on the coast of British Columbia and in a somewhat more restricted area at the north end of Vancouver I. in Queen Charlotte Strait. Further detailed work is in progress in the Strait of Juan de Fuca at the south end of Vancouver I. between Vancouver I. and northern Washington. The study in Queen Charlotte Strait forms the major part of this paper.

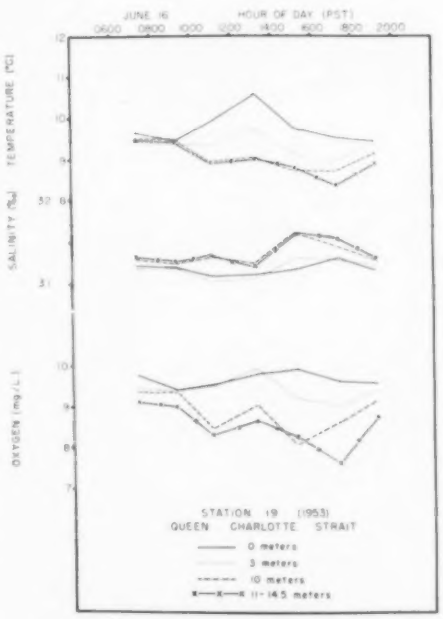

FIG. 13. Fluctuations in temperature, salinity, and oxygen at various depths near Malcolm Island at station 19 (1953).

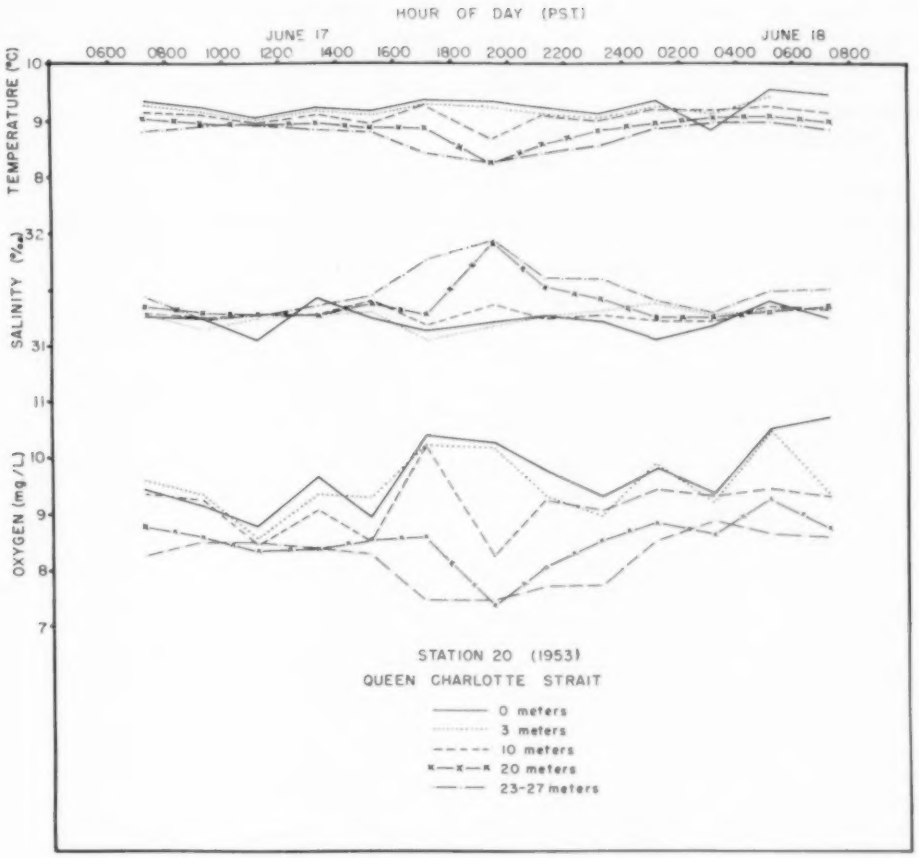

FIG. 14. Fluctuations in temperature, salinity, and oxygen at various depths near Malcolm Island at station 20 (1953).

The more detailed physical and chemical data presented in this paper for the Queen Charlotte Strait area were obtained during two cruises, one (53/1) on the C.G.M.V. "Cancolim II" in 1953 (anon., 1955*a*) and the other (56/1) on the C.N.A.V. "Ehkoli" in 1956 (anon., 1956*a*). The stations occupied during these two cruises are indicated in Figures 5 and 6, respectively. Further less detailed observations were made on a cruise (57/6) in May, 1957, on the C.N.A.V. "Clifton" (anon., 1958). In analyzing the seasonal characteristics and annual fluctuations of temperature and salinity that occur, reference has been made to the data obtained in the area from the daily records (anon., 1944, 1946, 1948*b*, 1949, 1950, 1951, 1952*b*, 1953*a*, 1955*c*, 1956*c*) and data reports of the Hecate Strait Project (anon., 1955*b*, 1955*d*, 1955*e*, 1956*b*) of the Pacific Oceanographic Group. Meteorological data have been obtained from the Meteorological Observations in Canada (anon., 1953*b*), and tidal data were taken from the Pacific Coast Tide Tables (anon., 1952*a*). Chart data have been taken from charts of the Canadian Hydrographic Office and the British Admiralty. Some additional physical and chem-

ical (anon., 1954; Pickard and McLeod, 1953) and geological data (Dawson, 1880, 1881*a*, 1881*b*, 1888, 1897; Bostock, 1948) have been referred to in the literature. Earlier biological observations and collections, which form part of the background for this paper, were made in the area in 1946 (anon., 1947, 1948*a*) and 1947 (Scagel, 1948). The results of a study of the phytoplankton and zooplankton collections which were also made during the same cruises will be presented in a subsequent paper.

GENERAL ECOLOGICAL CHARACTERISTICS OF COASTAL REGION

The Pacific Coast of Canada is ideally suited to a study of benthonic organisms and the effect of oceanographic factors on their distribution both in the intertidal and the subtidal zones. Although the coast of British Columbia (Fig. 1) is only about 600 mi. long, proceeding directly from the Strait of Juan de Fuca to Dixon Entrance, if all its various ramifications are included there is a coastline estimated at about 16,900 mi. in length. The tidal amplitude in this region is great, ranging from about 11 ft. at the southern boundary to nearly 26 ft. at the northern boundary. As a result of thorough mixing in the coastal region the upper zone in this area, except for a few local anomalies, is characteristically rather uniform in temperature at any one period and fluctuations occur within narrow limits. The annual range in temperature of the seawater near the surface is from about 6° to 18°C. On the other hand, because of the runoff from large rivers, especially through the long mainland inlets, there are conditions ranging from practically fresh water at one extreme to full ocean salinity of about 34 ‰ at the other.

Throughout the coast the physical nature of the substratum, ranging from mud and sand at one extreme to solid rock at the other, determines to a large extent the organisms which are found in a specific area. However, a comparison of the flora and fauna on various types of bottom is possible in a number of regions which are otherwise oceanographically rather similar. This permits a correlation of the distribution of a wide variety of plants and animals with other physical and chemical factors of the environment. The oceanographic conditions characteristic of the coast provide an ideal area in which to study the distribution of marine benthonic organisms particularly in relation to salinity over a rather extensive geographic area.

GEOLOGICAL CHARACTERISTICS

General Coast Features

The Coast Mountains of British Columbia, which run along the whole length of the prov-

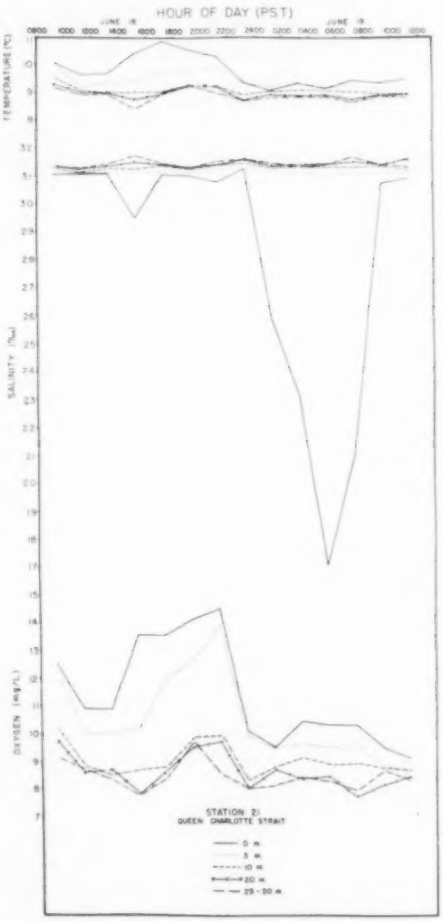

FIG. 15. Fluctuations in temperature, salinity, and oxygen at various depths near the Klucksiwi River at station 21 (1953).

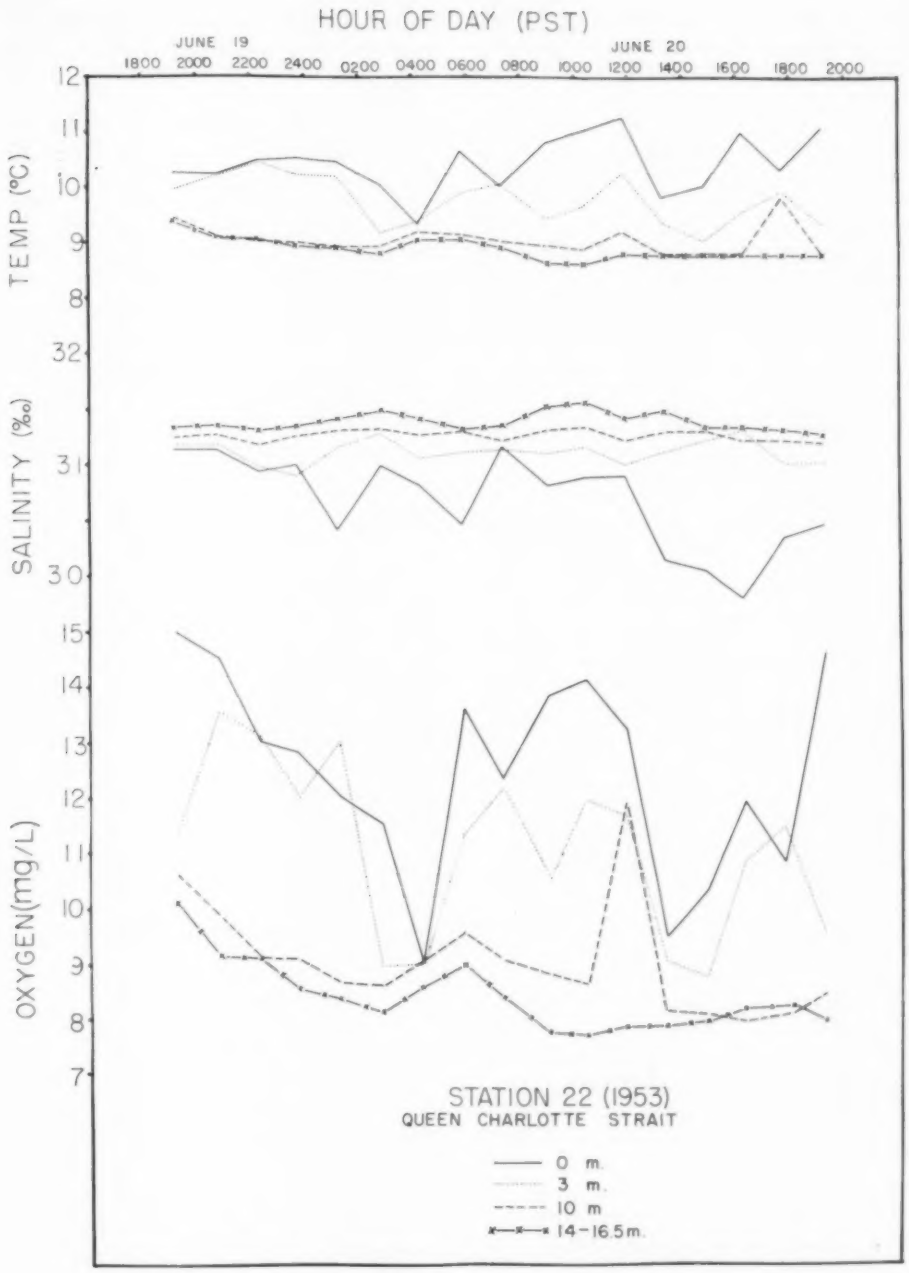

FIG. 16. Fluctuations in temperature, salinity, and oxygen at various depths near the Klucksiwi River at station 22 (1953).

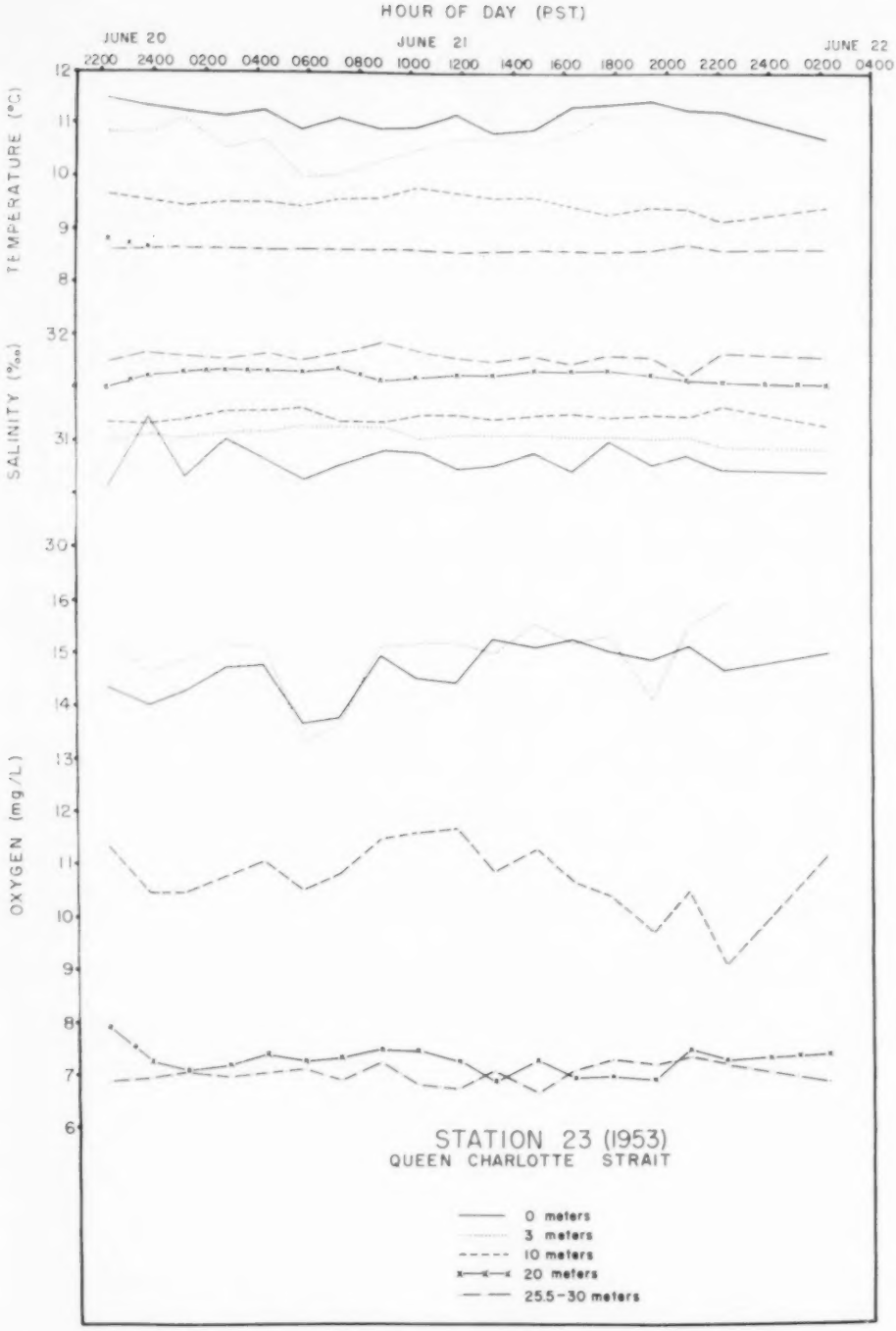

FIG. 17. Fluctuations in temperature, salinity, and oxygen at various depths near Deer Island at station 23 (1953).

ince with an average width of about 100 mi., constitute the mainland coast. Although not as rugged as elsewhere in the Cordillera, the western side of the Coast Mts. rises from the sea precipitously to summits in places exceeding 8,000 or 9,000 ft. Several rivers, which rise in the plateau country to the eastward, flow completely across this range to the Pacific, where the lower parts of their valleys, as well as those of many streams originating in the mountains themselves, continue in the extensive system of fjords along the mainland of British Columbia (Fig. 1). These sediment-filled systems of valleys with steep slopes and numerous deltas can be traced in some places even through the coastal archipelago, which represents a partly submerged margin of the Coast Mountains. West of the Coast Mountains, and in a partly submerged condition, lies another chain, the Insular Mountains, of which Vancouver I. and the Queen Charlotte Islands are projecting ranges. This outer chain stands on the edge of the continental platform with the great depths of the Pacific seaward from it. Between these

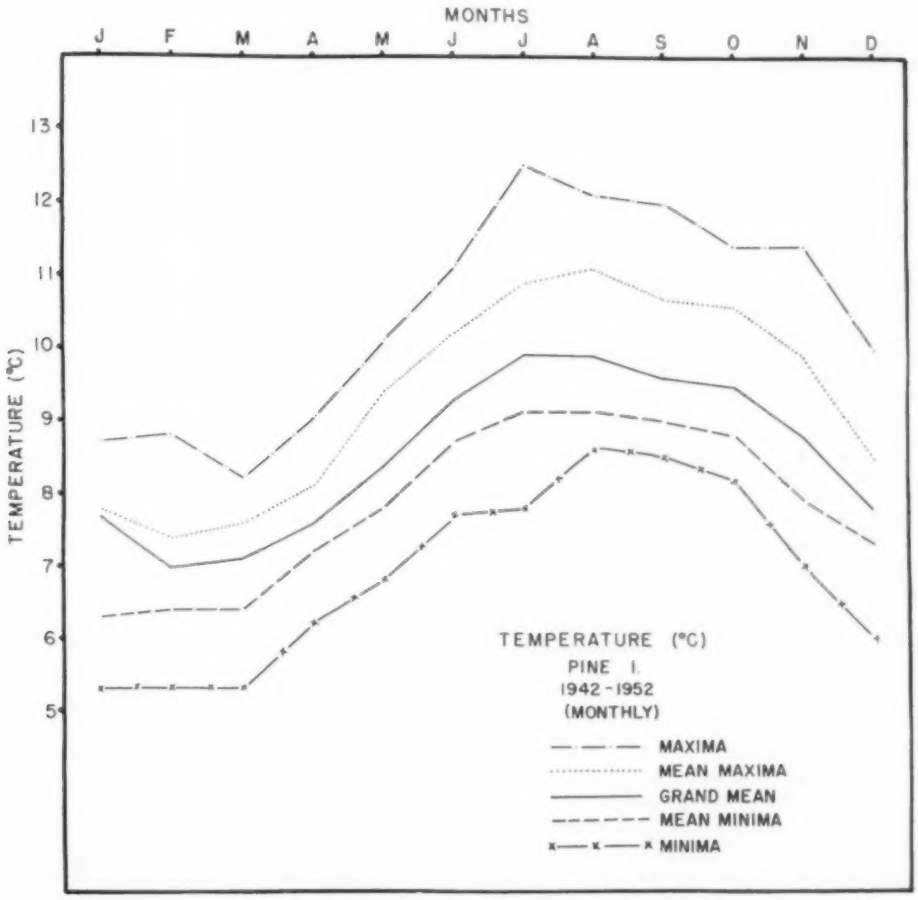

FIG. 18. Monthly temperatures of seawater at Pine Island for the period 1942–52.

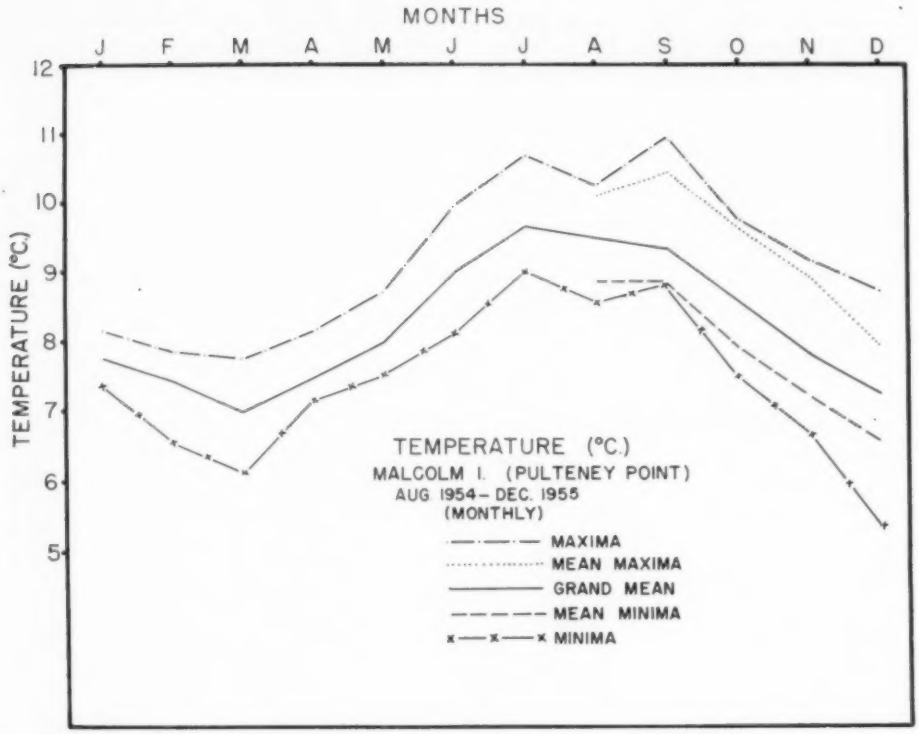

FIG. 19. Monthly temperatures of seawater at Pulteney Point, Malcolm Island, for the period 1954–55.

two ranges lies the Coastal Trough, part of a great depression extending intermittently northwestward from the Gulf of California through the Puget Sound–Williamette lowland and on into Alaska. In British Columbia this great valley is largely submerged and comprises the extensive areas of the Strait of Georgia, Queen Charlotte Strait, Queen Charlotte Sound, and Hecate Strait (Fig. 1).

The Coast Mountains consist largely of Mesozoic rocks ranging from Triassic to early Tertiary and are composed of principally granitic rocks with some included masses of Mesozoic and Palaeozoic strata. The rocks of the Vancouver I. Ranges are composed conspicuously of masses of Triassic and Jurassic lava and volcanic products, lesser contemporaneous sediments with subordinate amounts of later granitic rocks, and marine and continental Cretaceous

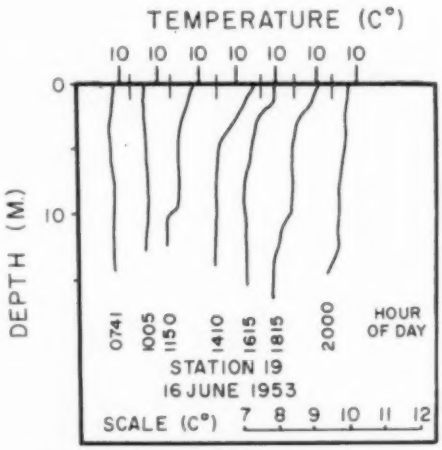

FIG. 20. Temperature profiles at station 19 (1953) near Malcolm Island from bathythermograph traces.

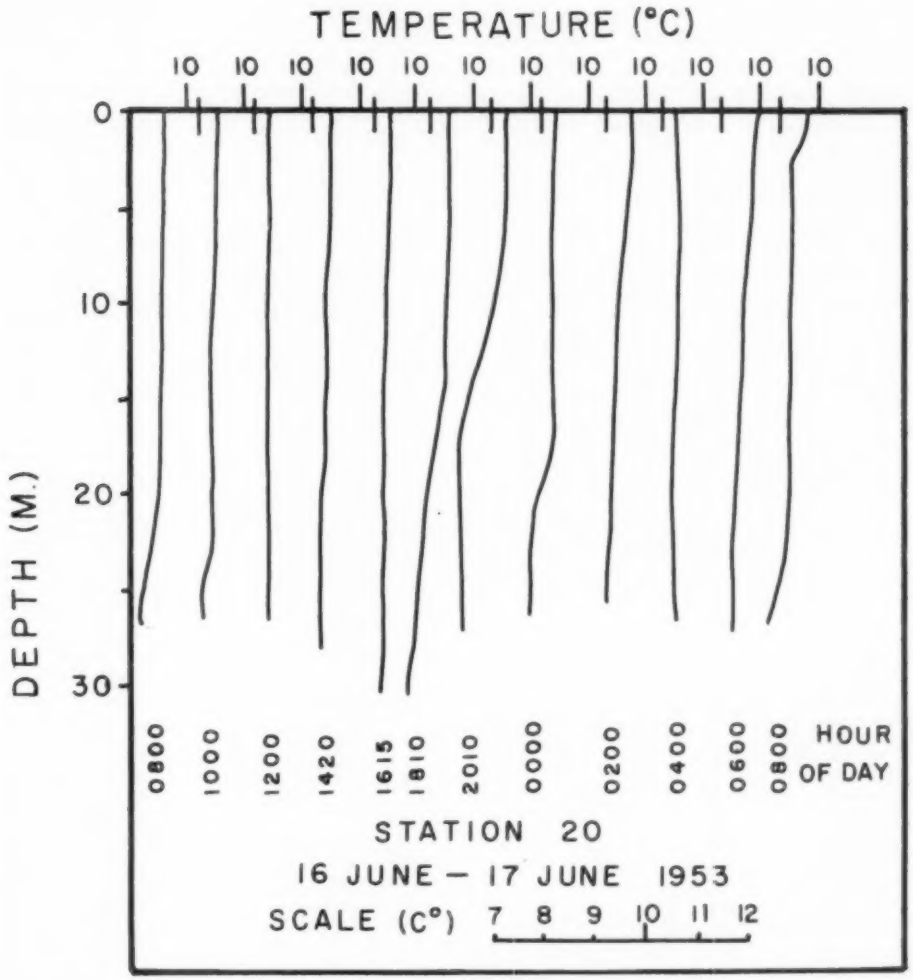

FIG. 21. Temperature profiles at station 20 (1953) near Malcolm Island from bathythermograph traces.

sediments which have participated in its folding. Horizontal Miocene beds occur along some parts of the shore.

General Features of Queen Charlotte Strait

Along the mainland portion of Queen Charlotte Strait (Figs. 1, 3) the rocks are chiefly Jurassic and intrusive, composed of granodiorite, chiefly quartz diorite. Parts of the island groups near the entrance to the Strait, including Hope I. and Nigei I., include some intrusive rocks similar to those on the mainland side, but the major part of the north end of Vancouver I. is composed of Triassic to Jurassic rocks. In this latter region argillites, lavas, tuffs, breccia, sandstones, and limy siltstones are common. A smaller por-

tion of the east coast of Vancouver I. from Hardy Bay southward almost to Johnstone Strait is Cretaceous (chiefly Upper Cretaceous), with shales and sandstones.

The rocks are heavily glaciated throughout almost the whole coastal area. The Queen Charlotte Strait area was heavily glaciated during the Pleistocene, which fact is particularly evident in the vicinity of Deer I., where northwestern slopes are comparatively rough in contrast to the grooved and polished vertical or near vertical faces on southeastern parts. Well-stratified deposits of clays, silts, and sands occur, particularly toward the east end of the Strait and along the Vancouver I. side. Cormorant I., Harwood I., and Malcolm I. are also examples of these deposits. In some places cliffs of these deposits border the shoreline, with extensive accumulations of boulders at the base. In such regions the boulders, which occur in great abundance along the beaches, are probably erratics derived from morainic material.

Although the detailed geology of Queen Charlotte Strait region is not well known supratidally, it is even less well known subtidally. The general features described, however, indicate the wide variety of substrata available for the attachment of benthonic organisms, particularly in the intertidal and shallower subtidal zones. This variety in the physical nature of the sub-

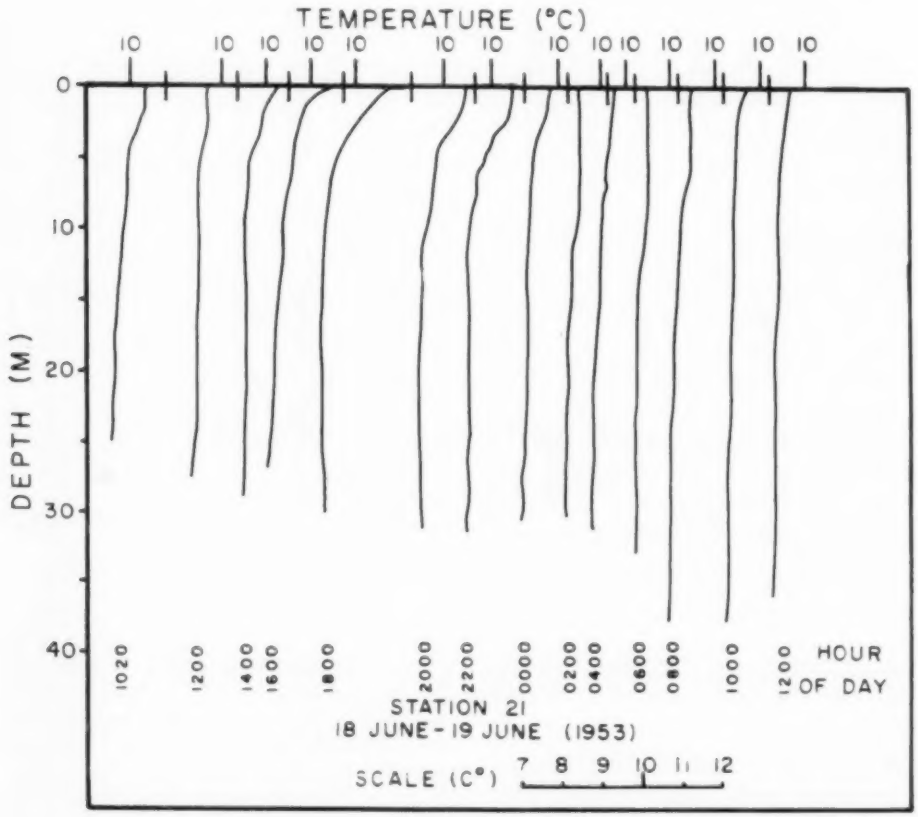

FIG. 22. Temperature profiles at station 21 (1953) near Malcolm Island from bathythermograph traces.

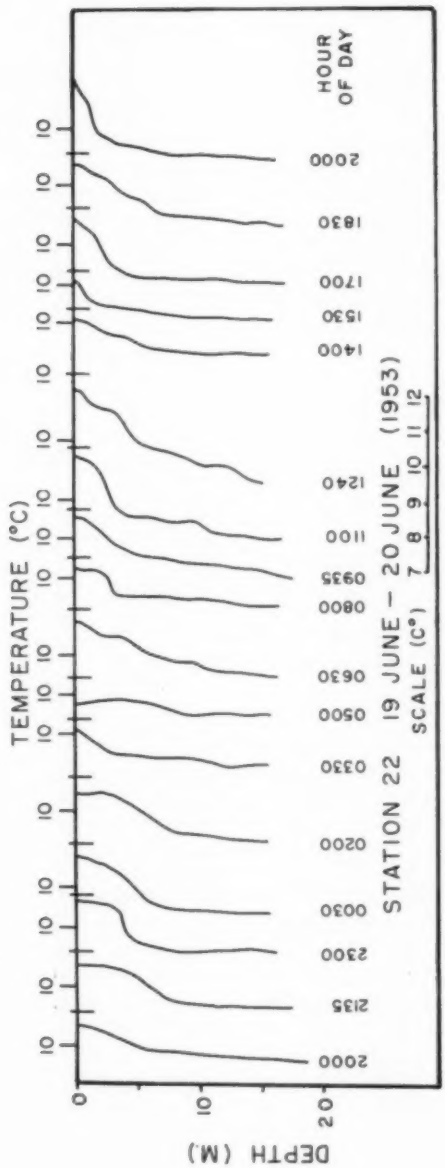

FIG. 23. Temperature profiles at station 22 (1953) near Malcolm Island from bathythermograph traces.

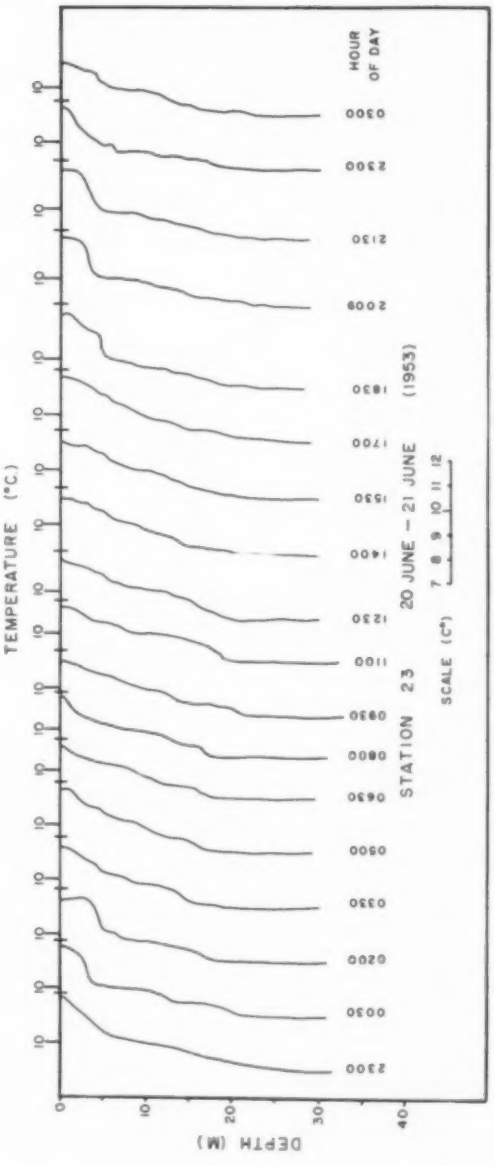

FIG. 24. Temperature profiles at station 23 (1953) near Deer Island from bathythermograph traces.

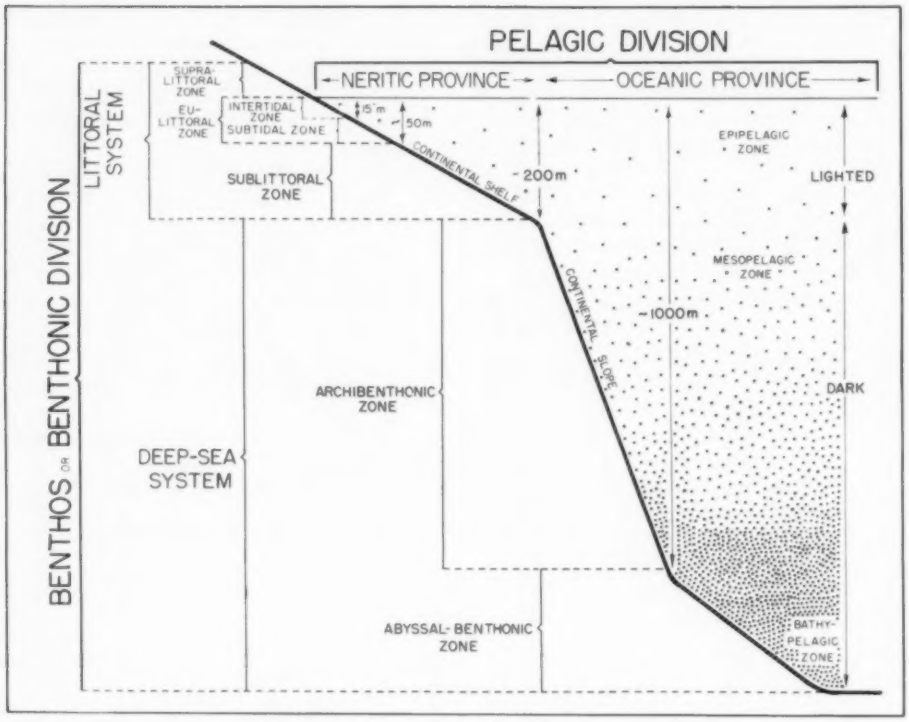

FIG. 25. Diagrammatic representation of regions of marine habitat (modified after Ekman, 1935).

stratum is apparent not only geographically in the area but also vertically. In the deeper water soft mud bottoms predominate but sand and gravel are also found, and in the shallower areas sand, mud, gravel, pebbles, boulders, and solid rock are all found to varying extent, particularly along the Vancouver I. side of the Strait. In the shallower regions, however, a solid rock or bouldery substratum predominates. The nature of this rocky substratum in Queen Charlotte Strait is equally varied. There are igneous as well as sedimentary and metamorphosed substrata. There are basalts, dolerites, trachytic rocks, hard sandstones or quartzites, shales, conglomerates, argillites, fine-grained to crystalline, commonly cherty limestones mixed with feldspathic rocks, and dioritic and granitic fragments are also common.

The preceding brief summary of the general geological features of the area indicates the present status of published knowledge (Bostock, 1948; Dawson, 1880, 1881*a*, 1881*b*, 1888, 1897) concerning the Queen Charlotte Strait region.

Bottom Topography of Queen Charlotte Strait

Although soundings are still incomplete for the area, a study of the bottom topography (Fig. 2) in Queen Charlotte Strait indicates extensive shallows, particularly along the Vancouver I. side of the Strait and around Malcolm I. In this region an abundant and varied intertidal and subtidal flora and fauna are supported. In the central part of the Strait and between Nigei and Vancouver islands (Fig. 2), there are deeper channels exceeding 100 fathoms. The water in these deeper channels is not continuous, however, with the deep waters of the main-

land inlets and Johnstone Strait, and exhibits physical and chemical properties quite distinct from the latter (Figs. 3, 4).

PHYSICAL CHARACTERISTICS

Hydrographic Conditions in Queen Charlotte Strait

The salinity distribution near the surface (Figs. 7–10) in Queen Charlotte Strait suggests a general circulation in a counter-clockwise fashion. The runoff from the mainland inlets along the north shore and at the east end of the Strait, particularly from Knight Inlet at the east end, contributes large volumes of fresh water which tends to move seaward at the surface, mixing as it progresses along the north shore into Queen Charlotte Sound with the deeper more saline water below. The more saline water from the open ocean and Queen Charlotte Sound moves into the Strait centrally as well as along the Vancouver I. side of the Strait and along the north side of Malcolm I. The intrusion of high salinity water along the deep channels in the central part of the Strait is also apparent. This general pattern of salinity distribution, with fluctuations to varying degrees near the surface, is pronounced in the upper zone to a depth of at least 20 m. (Figs. 7–10).

Although strong winds may assist in the movement of water near the surface there is clear evidence at times of the movement of water against the wind and there are strong tidal currents throughout the region. The cur-

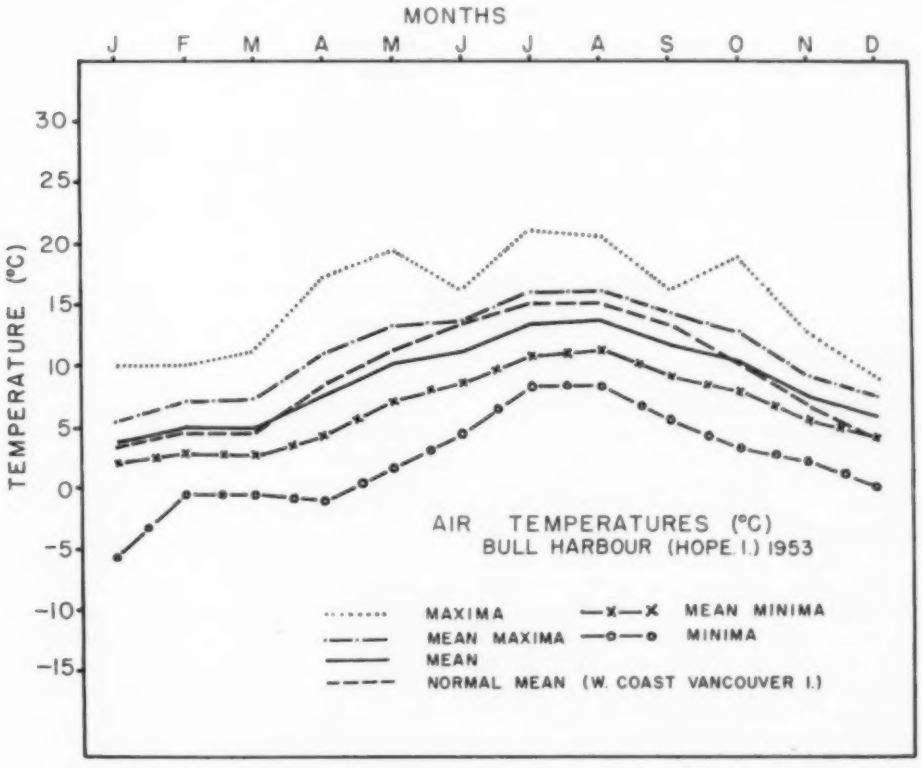

FIG. 26. Monthly air temperatures at Bull Harbour, B. C., for 1953.

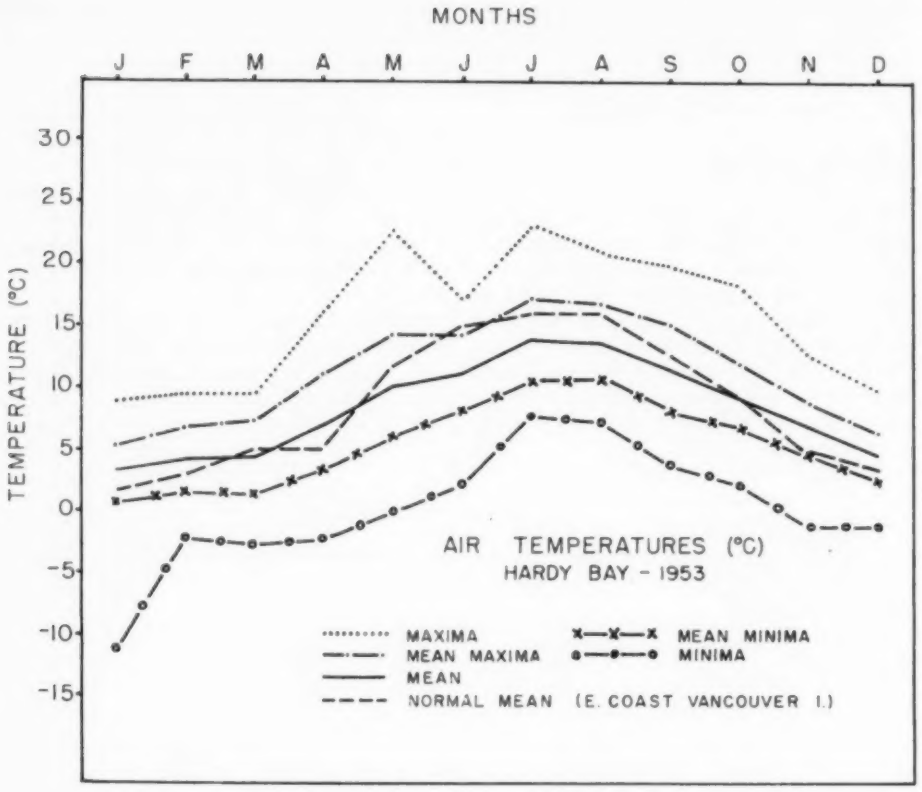

FIG. 27. Monthly air temperatures at Hardy Bay, B. C., for 1953.

rent velocities involved vary considerably but at times may reach at least 80 cm/sec from near the surface to a depth of 20 m., and in deeper portions of the Strait, although generally much less, they may attain as much as 57 cm/sec at a depth of 125 m.

An analysis of surface salinity data over a 10-year period (Fig. 11) from Pine I. Lighthouse, which is near the entrance to Queen Charlotte Strait, indicates a salinity maximum of about 33 ‰ and a minimum of about 30 ‰, with an annual mean of 31.75 ‰. Although this station is not characteristic of the Strait itself, the data available probably give a reasonable approximation of the annual salinity fluctuations for the Strait. Insufficient data are available from Pulteney Point on Malcolm I. to analyze the seasonal fluctuations more precisely in the central region of the Strait, but for the period available (Fig. 12) a range of about 28 ‰ to 32 ‰ with an annual mean of 21.50 ‰ is indicated.

Seasonal data indicate that near the surface the distribution of salinity throughout the year follows the same general pattern, decreasing toward the mainland and being higher along the Vancouver I. side of the Strait. At any one point, however, there is a general decrease in salinity in time from the maximum in April to a minimum in midsummer, when the maximum runoff from the mainland inlets occurs. The winter salinity may be somewhat modified near

the surface during the period of maximum precipitation, which may reduce salinity near the surface.

The minor extent of fluctuations that occur in the salinity distribution in the upper 20 m. is indicated by data taken at a number of anchor stations (Figs. 13–17). These fluctuations are greatest at or near the surface and, in certain instances, as near the Klucksiwi River (Fig. 15), show the influence of fresh-water inflow of a more localized nature.

A comparison of the temperature–salinity characteristics of various parts of the Strait and the connecting bodies of water by means of T–S diagrams (Figs. 3, 4) indicates the discreteness of the water masses typical of Johnstone Strait, mouth of Knight Inlet, and Queen Charlotte Sound. The T–S diagrams for Queen Charlotte Strait indicate a characteristically intermediate condition between these extremes in properties of temperature and salinity for the greater part of the Strait.

An analysis of surface temperature data over a 10-year period (Fig. 18) from Pine I. Lighthouse, which is near the entrance to Queen Charlotte Strait, indicates a temperature maximum of about 12°C. and a minimum of about 5°C., with an annual mean of 8.6°C. Although this station, as already indicated, is not characteristic of the Strait itself in all respects, it probably gives a reasonable approximation of the annual temperature fluctuations. Insufficient data are available from Pulteney Point on Malcolm I. to analyze more precisely the seasonal

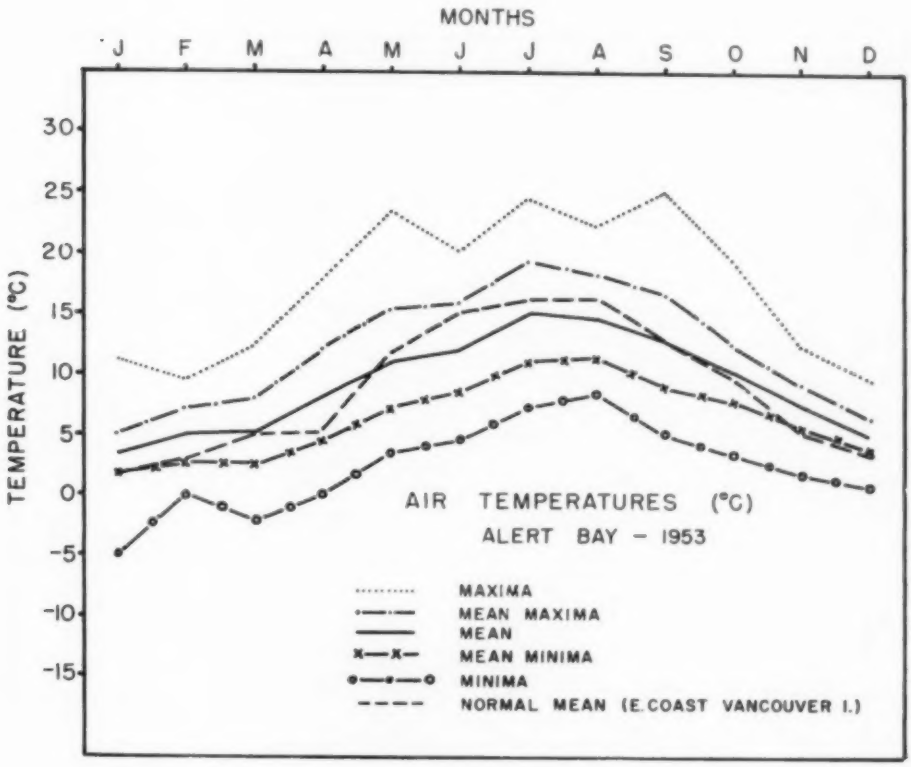

FIG. 28. Monthly air temperatures at Alert Bay, B. C., for 1953.

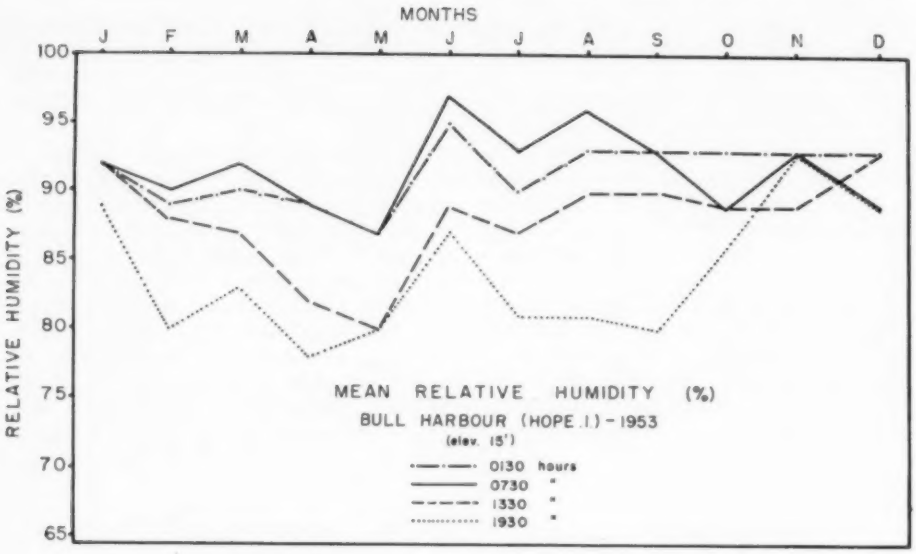

FIG. 29. Monthly relative humidity at Bull Harbour, B. C., for 1953.

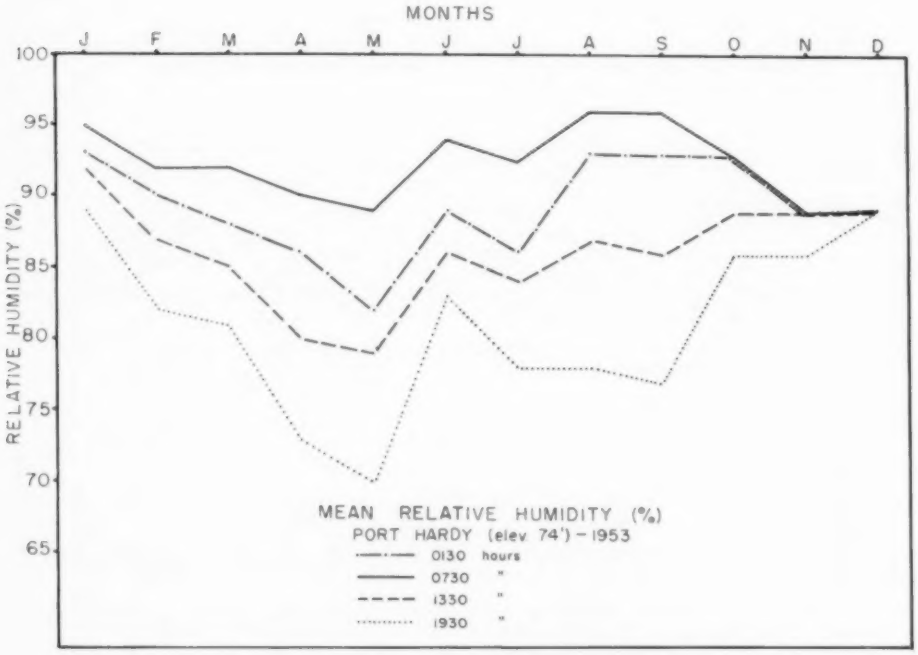

FIG. 30. Monthly relative humidity at Port Hardy, B. C., for 1953.

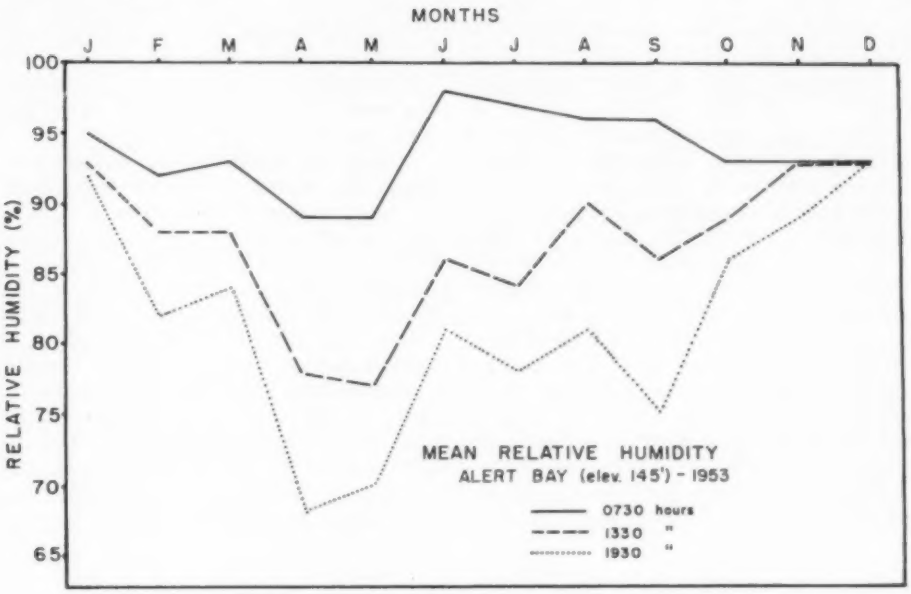

FIG. 31. Monthly relative humidity at Alert Bay, B. C., for 1953.

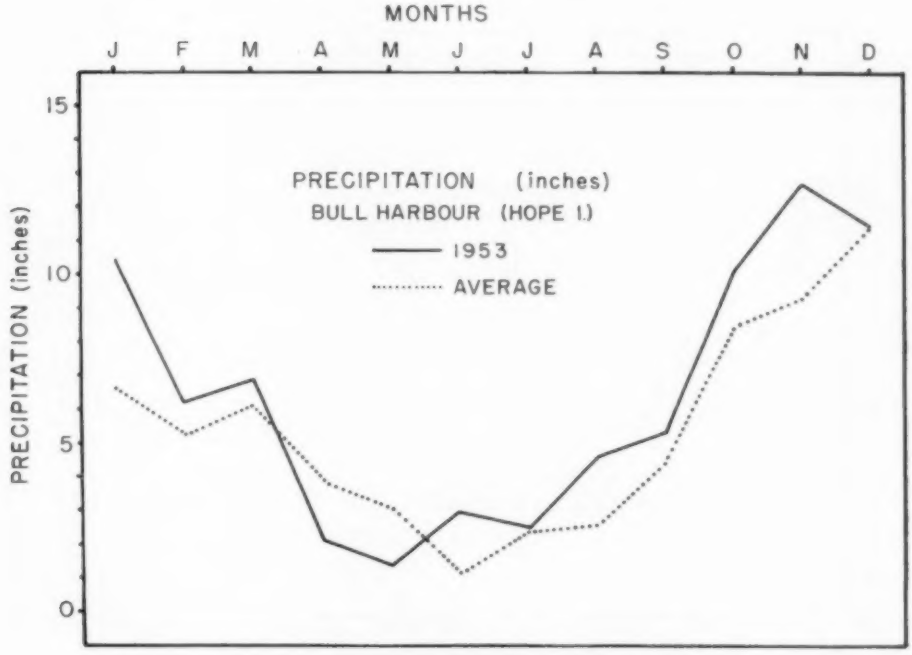

FIG. 32. Monthly precipitation at Bull Harbour, B. C., for 1953.

fluctuations in the central region of the Strait, but for the period available (Fig. 19) a range of from about 5° to 11°C. with an annual mean of 8.25°C. is indicated.

The temperature distribution with depth, as shown by bathythermograph records taken at shallow anchor stations, indicates a well-mixed region near the surface along Vancouver I. and Malcolm I. (Figs. 20–24). Except for slight anomalies the water is generally almost isothermal, with temperatures during this period of observation seldom above 11°C. at the surface and falling to not less than 8°C. at a depth of 20 m. As indicated from the anchor stations, there are no marked changes with time in this general picture of the vertical distribution of temperature, and at any one depth the fluctuations indicated were less than 2 C.° (Figs. 13–17).

However, there is a slight difference (usually not more than 1 C.°) in temperature at the surface at most times of the year, with the water along the Vancouver I. side being warmer than that along the mainland side of the Strait. This is a result of the inflow of colder, less saline water from the mainland inlets.

Seasonal data indicate that in general during the summer months the temperature at the surface is seldom above 10°C. and at a depth of 20 m. is seldom above 9°C. During the winter months it is seldom below 7.5°C. at the surface but may be about 7°C. at a depth of 20 m. This picture of the vertical temperature distribution is somewhat modified during the winter as a result of surface cooling of the water down to a depth of about 20 m. and a temperature inversion has been observed in January which disappears by April. During this early period the water at the depth of 20 m. and, in places, even to a depth of 400 m., may be warmer than that in the upper 20 m. by as much as 1 C.° and

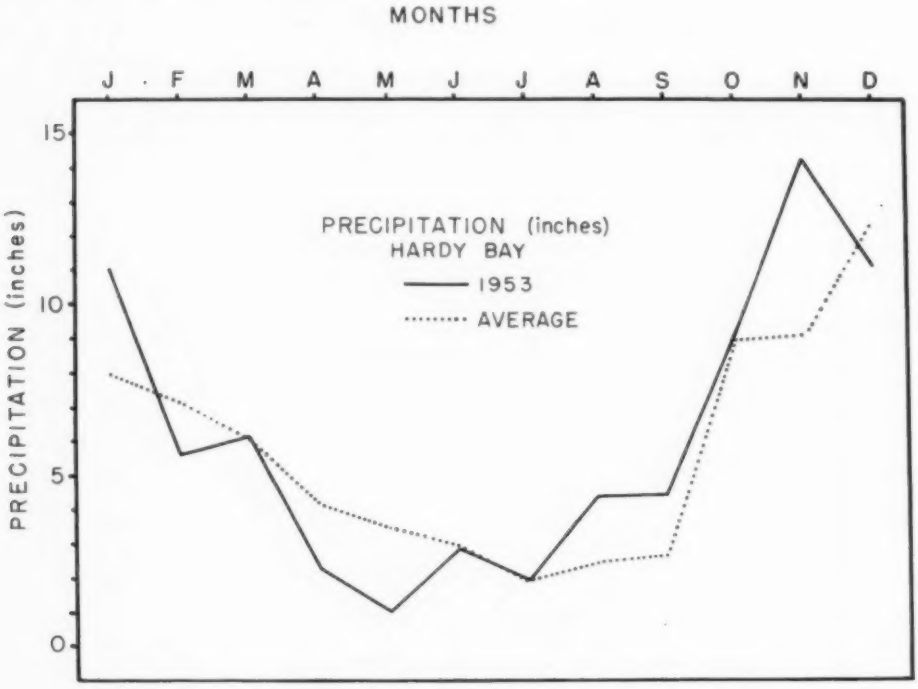

FIG. 33. Monthly precipitation at Hardy Bay, B. C., for 1953.

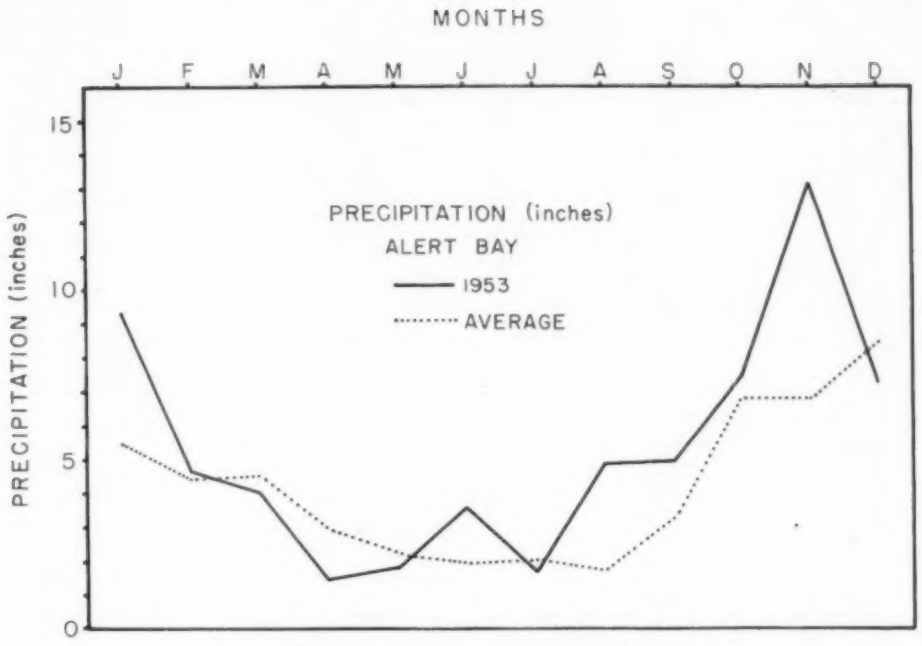

FIG. 34. Monthly precipitation at Alert Bay, B. C., for 1953.

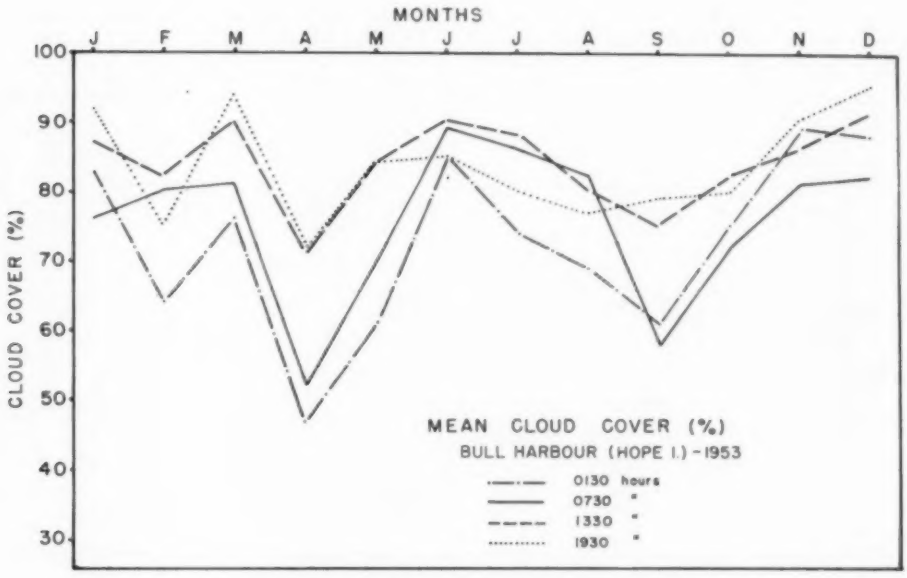

FIG. 35. Monthly cloud cover at Bull Harbour, B. C., for 1953.

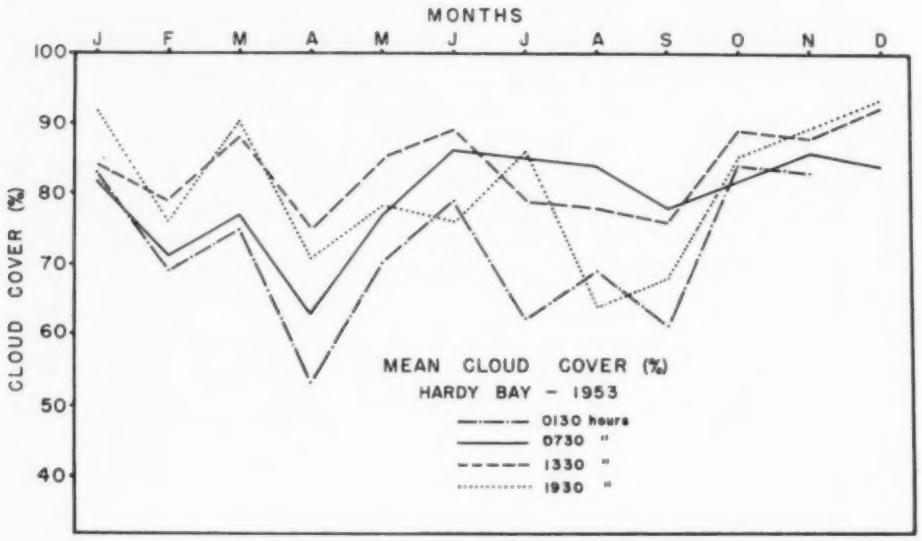

FIG. 36. Monthly cloud cover at Hardy Bay, B. C., for 1953.

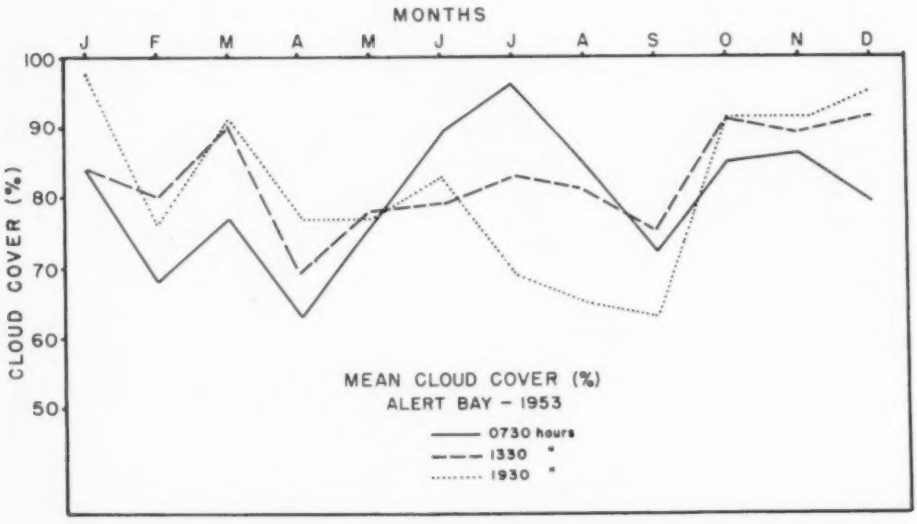

FIG. 37. Monthly cloud cover at Alert Bay, B. C., for 1953.

then fall to a lower temperature again, beneath this warmer upper layer, down to between 6° and 7°C. in the deeper regions.

Thus the environment presented to the intertidal and immediate subtidal zones (see Fig. 25 for terminology) appears to be a relatively stable one as far as the temperature of the seawater is concerned.

Meteorological Conditions

The intertidal region, however, during periods of exposure, is subjected to a varying degree to meteorological conditions, particularly fluctuations in temperature and precipitation, which must be considered in assessing the environment of organisms in this region. A comparison of the meteorological data (air temperatures, precipitation, mean relative humidities, and mean cloud cover) available for the coast of British Columbia, particularly from Bull Harbour (Hope I.), Hardy Bay, and Alert Bay, gives some picture of the meteorological conditions at the northeast end of Vancouver I. (Figs. 26–37).

Along the coast, air from the maritime Pacific Ocean is usually present and results in mild winters and cool summers. Holding a high moisture content, this air does not become extremely hot or cold. However, occasional outbreaks of continental air (polar) from the interior of the

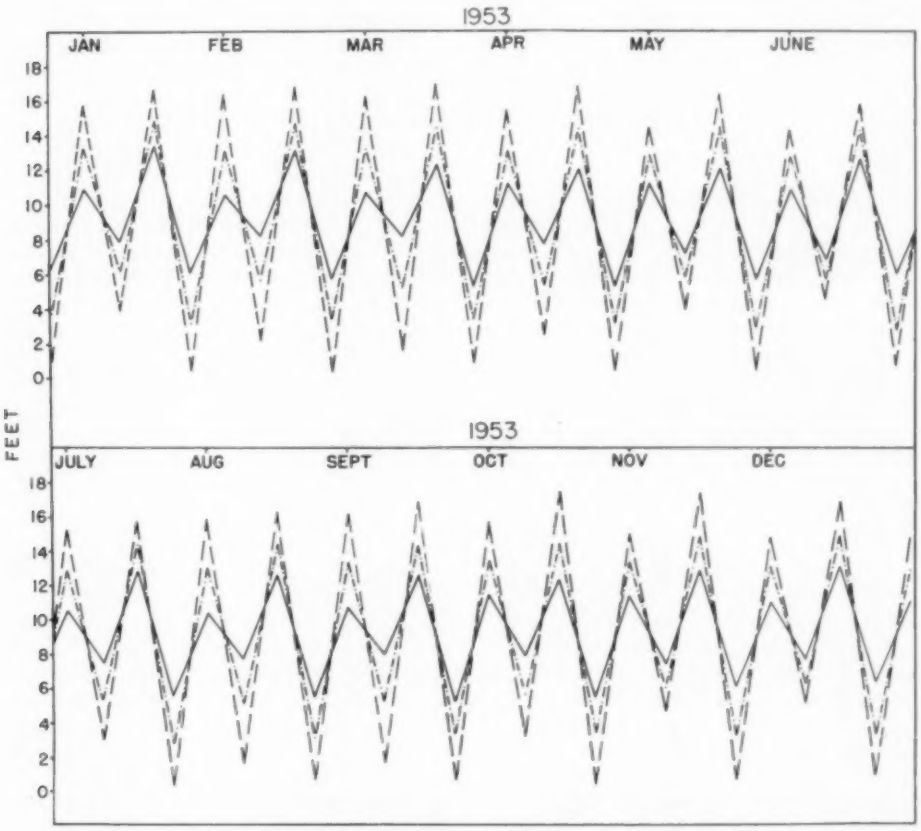

FIG. 38. Monthly summary of tidal features at Hope Island for 1953 (see Figure 39 for significance of lines).

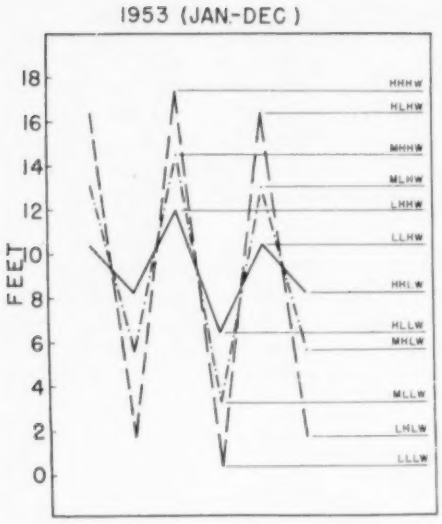

FIG. 39. Summary of tidal features for 1953.

continent bring cold periods during the winter, although generally the Coast and Cascade mountains provide considerable protection. Along the outer coast, the maritime conditions, which are present almost continually, result in high precipitation, prolonged cloudiness, and small ranges in temperature—the typical conditions prevailing in the vicinity of Hope I. (Figs. 26, 29, 32, 35) and Hardy Bay (Figs. 27, 30, 33, 36), despite the fact that these points are somewhat on the lee side of Vancouver I. Along the inner coast and the lee side of Vancouver I., where there is some protection from the maritime influence, precipitation and cloudiness are somewhat reduced and ranges in temperature are somewhat increased, as at Alert Bay (Figs. 28, 31, 34, 37).

The number of frost-free days in the whole Queen Charlotte Strait region averages 200–250 in a year. In both outer and inner regions there are no months with all temperatures ranging below 0°C. In the outer coastal region 4 to 5 months have temperatures above 10°C., and in the inner coastal region 5 to 6 months have temperatures above 10°C. In the outer coastal region, depending upon the locality, the mean monthly air temperatures for January are 1.7° to 4.4°C., and for July 13.3°C., and the mean daily temperatures are —1.1° to 1.7°C. and 15.6° to 18.9°C. for the same months, respectively. In the inner coastal region, depending upon the locality, the mean monthly air temperatures for January are 1.7° to 3.3°C., and for July 15.6° to 18.3°C., and the mean daily temperatures are —1.1° to 0°C. and 21.1° to 23.9°C., respectively, for the same months.

Although some restricted regions of British Columbia on Vancouver I. average as much as 264 in. of rain, in the Queen Charlotte Strait region the annual rainfall averages between 40 and 60 in. at the inner end (including Alert Bay and Malcolm I.), with between 5–10 per cent as snow, and between 60 and 100 in. at the outer end (including Hope I. and Port Hardy), with less than 5 per cent as snow. The period of minimum rainfall is in the summer,

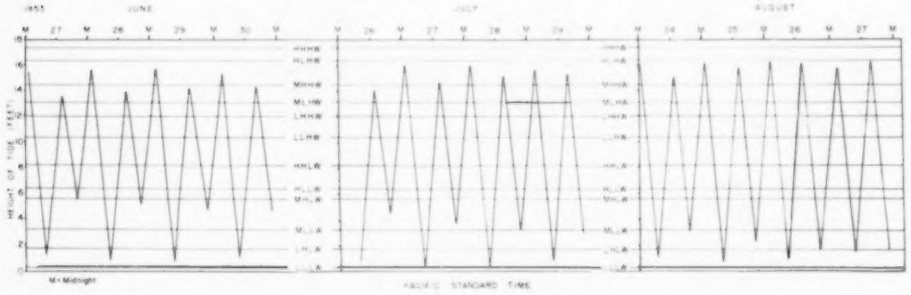

FIG. 40. Tidal features for the periods of greatest exposure during summer months of 1953.

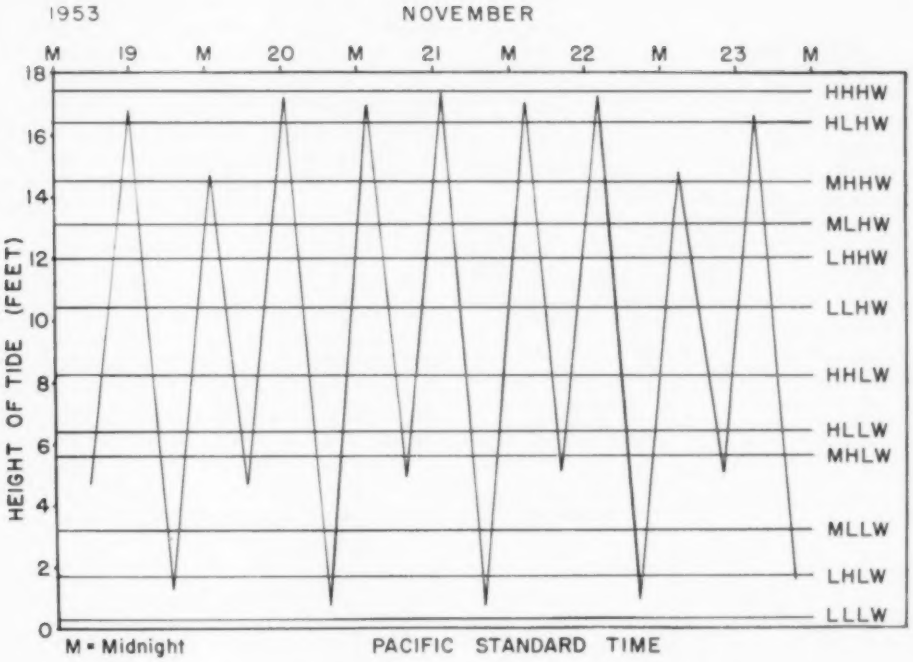

FIG. 41. Tidal features for period of greatest exposure during winter months of 1953.

with between 2–3 in. on the average falling during August in the Strait, and the maximum rainfall occurs in the winter, with between 9–13 in. on the average in December.

Near the entrance of the Strait, especially along the north side of Hope I., conditions of heavy surf generally prevail. Even when there is no sea a heavy swell is common. Farther down in the Strait to the south and east there is an area protected by scattered islands and reefs near the entrance, from the heavy swell from the open ocean, but this whole area is subject to strong westerly winds in the summer months and to even stronger southeasterly winds during the winter months, so that the Strait is generally subjected to strong wave action and wind mixing. During the period mid-September to mid-May the southeasterly winds are predominent and blow at speeds frequently up to 40 m.p.h. and occasionally higher. During the period mid-May to mid-September the westerly winds predominate and blow at speeds up to 25 m.p.h. Particularly during this latter period, however, there may be considerable calm periods, especially during the morning hours, followed by strong seas which reach a peak about 1600 hrs. and then drop rapidly to relative calm by 2000 hrs.

Tidal Characteristics

The tidal amplitude in the vicinity of Hope I. is usually about 17 ft. and the highest on record (37 years) was almost 19 ft. (December, 1941). An extensive intertidal flora and fauna is exposed during low tide periods in this zone. Continuous tidal data are recorded since 1949 at Alert Bay, near station 8 (Fig. 6). At the north end of Vancouver I. the tides are semidiurnal and only moderately declinational, and thus springs and neaps are distinguishable (Figs.

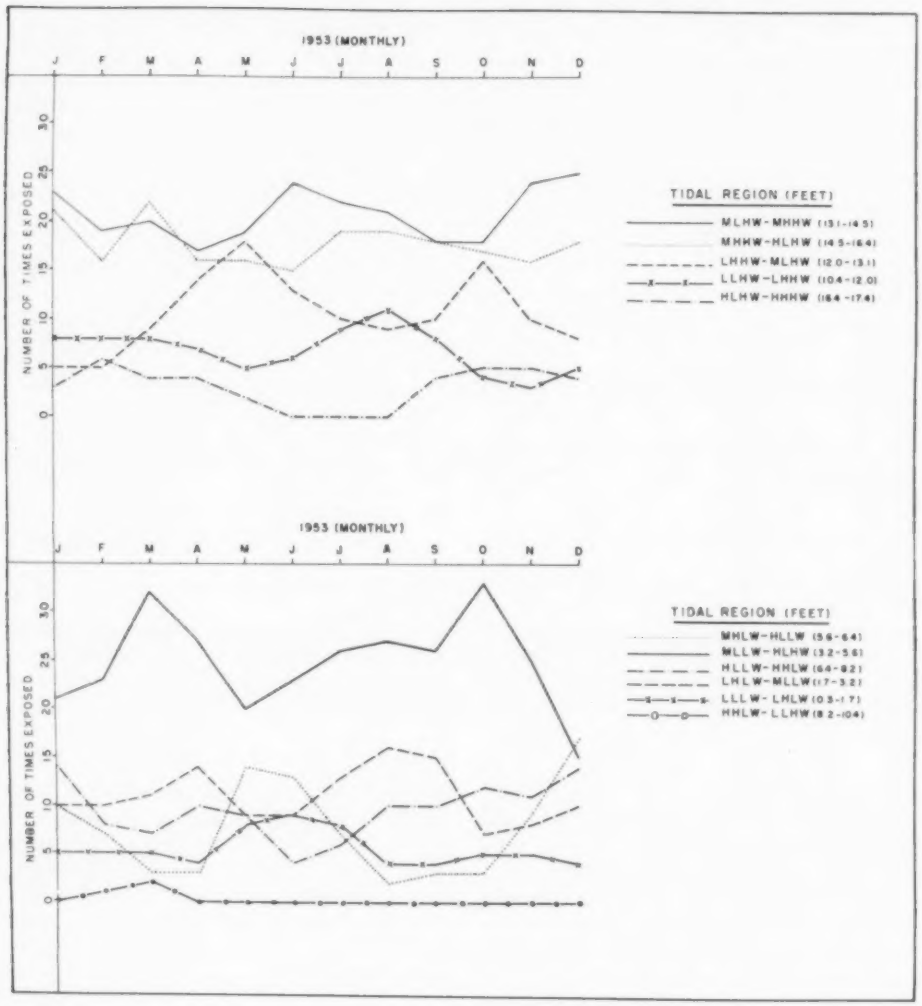

FIG. 42. Diagram showing number of times each month during 1953 various levels in the intertidal zone were exposed.

38–41). Twice a month there are two tides a day which are about equal, and in the intervals between there is a much greater inequality in the height of any two successive low waters than between the two high waters of the same day. During the summer months (Fig. 40) the lowest low waters occur during daylight hours and during the winter months (Fig. 41) the lowest low waters occur late at night or early in the morning.

The number of times during the year when each of the various levels recognized (Fig. 39) are exposed is indicated in Figure 42, and the number of days of continuous exposure of the

upper portions of the intertidal zone are shown in Figure 43. The number of times (and per cent) these levels are exposed (Fig. 44) and submerged (Fig. 45) are also presented in an attempt to indicate possible critical levels. The tide levels are referred to in feet above or below the datum (zero point) which, for the coast of British Columbia, is the level of lowest normal tides.

Chemical Characteristics

During the summer months, when plant production is at its peak in Queen Charlotte Strait, the surface zone may be supersaturated with oxygen; values in excess of 15 mg/l are frequently encountered. The maximum values generally prevailing near the surface and to a depth of 20 m. are between 7 and 10 mg/l. During the summer months the values are somewhat higher than in the winter. The maximum concentration of oxygen occurs at a depth between 2 and 5 m. (Figs. 46, 47), rather than right at the surface during the summer, and is related to the region of maximum phytoplankton activity. The water throughout most of the Strait has a higher oxygen content near the surface (Figs. 46, 47) than in Queen Charlotte Sound or in the adjacent connecting mainland channels. Although marked fluctuations occur locally in the upper 10 m., the general picture is more stable (Figs. 13–17) at greater depth.

Phosphate concentrations (PO_4–P) are not available for the winter months, but for the summer, during which minimum amounts are probably reached, the values present (Fig. 48) were between 0.5 and 2.0 mg.-at. per liter in the upper 20 m. The minima were generally in the upper 10 m. and most of the minima for the Strait and Queen Charlotte Sound were between 1.0 and 1.5 mg.-at. per liter.

BIOLOGICAL CHARACTERISTICS

Biological observations, extending over the length of the coast, indicate that there is a high degree of uniformity in the populations of many benthonic plants and animals extending from the Strait of Juan de Fuca to Dixon Entrance. This would be anticipated under such relatively uniform conditions of temperature. In attempting to correlate the distribution of some of these organisms with salinity characteristics, as well as other oceanographic factors, there are several areas on the coast which could be used for purposes of this study. Although some supporting observations have been made in the Strait of Juan de Fuca and Dixon Entrance, this paper is restricted largely to a consideration of the vicinity of Queen Charlotte Strait near the north end of Vancouver I.

Horizontal Distribution of Organisms in Queen Charlotte Strait

Biological observations have been made throughout the area although a more intensive study and collection has been undertaken at Hope I., Deer I., and in the vicinity of the Keogh River, the Klucksiwi River, and Malcolm I. These areas present a transition from Hope I., where the highest salinities are encountered, to the north and east sides of the Strait, where lowest salinities are found, with Deer I. and Malcolm I. being intermediate between these extremes. The distributions in the Strait of the more conspicuous organisms (Table 1) observed during this study are illustrated in Figure 49. Although both the marine algae and the invertebrate animals have been observed, the emphasis in this study is on the more conspicuous marine algae.

Some organisms in the area are more cos-

FIG. 43. Diagram showing number of days various levels in the intertidal zone were subjected to continuous exposure.

TABLE 1

LIST OF THE MORE CONSPICUOUS SPECIES OF MARINE BENTHONIC ORGANISMS IN QUEEN CHARLOTTE STRAIT

1. *Polyneura latissima* (Harvey) Kylin
2. *Chthamalus dalli* Pilsbry
3. *Tegula funebralis* (Adams)
4. *Acmaea instabilis* (Gould)
5. *Balanus cariosus* (Pallas)
6. *Endocladia muricata* (Harvey) J. Agardh
7. *Gloiopeltis furcata* (Postels et Ruprecht) J. Agardh
8. *Prionitis lanceolata* Harvey
9. *Prionitis lyallii* Harvey
10. *Erythrophyllum delesserioides* J. Agardh
11. *Petrocelis franciscana* Setchell et Gardner
12. *Hildenbrandia occidentalis* Setchell
13. *Opuntiella californica* (Farlow) Kylin
14. *Plocamium pacificum* Kylin
15. *Gigartina papillata* (C. Agardh) J. G. Agardh
16. *Gigartina sitchensis* Ruprecht
17. *Iridaea cordata* (Turner) Bory
18. *Iridaea heterocarpa* Postels et Ruprecht
19. *Halosaccion glandiforme* (Gmelin) Ruprecht
20. *Rhodymenia palmata* (Linnaeus) Greville f. *palmata*
21. *Gastroclonium coulteri* (Harvey) Kylin
22. *Microcladia borealis* Ruprecht
23. *Ptilota asplenioides* (Esper) C. Agardh
24. *Ptilota californica* Ruprecht
25. *Ptilota hypnoides* Harvey
26. *Hymenena setchellii* Gardner
27. *Hymenena flabelligera* (J. Agardh) Kylin
28. *Cryptopleura ruprechtiana* (J. Agardh) Kylin
29. *Polysiphonia collinsii* Hollenberg var. *collinsii*
30. *Pterosiphonia bipinnata* (Postels et Ruprecht) Falkenberg var. *bipinnata*
31. *Laurencia spectabilis* Postels et Ruprecht
32. *Rhodomela larix* (Turner) C. Agardh
33. *Odonthalia floccosa* (Esper) Falkenberg
34. *Odonthalia washingtoniensis* Kylin
35. *Prasiola meridionalis* Setchell et Gardner
36. *Agardhiella coulteri* (Harvey) Setchell
37. *Saundersella simplex* (Saunders) Kylin
38. *Heterochordaria abietina* (Ruprecht) Setchell et Gardner
39. *Desmarestia intermedia* Postels et Ruprecht
40. *Desmarestia herbacea* Lamouroux
41. *Desmarestia media* var. *tenuis* Setchell et Gardner
42. *Desmarestia munda* Setchell et Gardner
43. *Soranthera ulvoidea* Postels et Ruprecht f. *ulvoidea*
44. *Myelophycus intestinale* Saunders
45. *Scytosiphon lomentaria* (Lyngbye) J. Agardh f. *lomentaria*
46. *Coilodesme bulligera* Stroemfelt
47. *Laminaria cuneifolia* J. Agardh f. *cuneifolia*
48. *Laminaria saccharina* (Linnaeus) Lamouroux f. *saccharina*
49. *Laminaria setchellii* Silva
50. *Pleurophycus gardneri* Setchell et Saunders
51. *Agarum fimbriatum* Harvey
52. *Agarum cribrosum* Bory
53. *Hedophyllum sessile* (C. Agardh) Setchell
    a. smooth form
    b. bullate form
54. *Postelsia palmaeformis* Ruprecht
55. *Lessoniopsis littoralis* (Farlow et Setchell) Reinke
56. *Pterygophora californica* Ruprecht
57. *Egregia menziesii* (Turner) Areschoug subsp. *menziesii*
58. *Fucus evanescens* C. Agardh f. *evanescens*
59. *Fucus gardneri* Silva f. *gardneri*
60. *Pelvetiopsis limitata* (Setchell) Gardner f. *limitata*
61. *Cystoseira geminata* C. Agardh
62. *Smithora naiadum* (Anderson) Hollenberg
63. *Porphyra perforata* J. Agardh f. *perforata*
64. *Farlowia mollis* (Harvey et Bailey) Farlow et *Setchell*
65. *Dilsea californica* (J. Agardh) O. Kuntze
66. *Gloiosiphonia californica* (Farlow) J. Agardh
67. *Nereocystis luetkeana* (Mertens) Postels et Ruprecht
68. *Macrocystis integrifolia* Bory
69. *Alaria nana* Schrader
70. *Alaria marginata* Postels et Ruprecht
71. *Alaria tenuifolia* Setchell f. *tenuifolia*
72. *Alaria valida* Kjellman et Setchell f. *valida*
73. *Bangia fuscopurpurea* (Dillwyn) Lyngbye
74. *Bossiella plumosa* (Manza) Silva
75. *Bossiella californica* (Decaisne) Silva
76. *Calliarthron regenerans* Manza
77. *Calliarthron schmittii* Manza
78. *Callithamnion pikeanum* Harvey var. *pikeanum*
79. *Callophyllis edentata* Kylin
80. *Callophyllis firma* Kylin
81. *Cladophora trichotoma* (C. Agardh) Kützing
82. *Spongomorpha coalita* (Ruprecht) Collins
83. *Codium fragile* (Suringar) Hariot
84. *Codium setchellii* Gardner
85. *Coilodesme californica* (Ruprecht) Kjellman
86. *Constantinea simplex* Setchell
87. *Constantinea subulifera* Setchell
88. *Corallina officinalis* var. *chilensis* (Harvey) Kützing
89. *Costaria costata* (Turner) Saunders
90. *Costaria mertensii* J. Agardh
91. *Cryptosiphonia woodii* J. Agardh
92. *Cumagloia andersonii* (Farlow) Setchell et Gardner
93. *Cymathere triplicata* (Postels et Ruprecht) J. Agardh
94. *Halicystis ovalis* (Lyngbye) Areschoug
95. *Pylaiella litoralis* (Lyngbye) Kjellman
96. *Leathesia difformis* (Linnaeus) Areschoug
97. *Haplogloia andersonii* (Farlow) Levring

TABLE 1 *(continued)*

98. *Ahnfeltia concinna* J. Agardh
99. *Rhodoglossum latissimum* J. Agardh
100. *Iridaea lineare* (Setchell et Gardner) Kylin
101. *Ahnfeltia plicata* (Hudson) Fries
102. *Schizymenia pacifica* Kylin
103. *Rhodoglossum affine* (Harvey) Kylin
104. *Flustrella corniculata* (Smitt)
105. *Mytilus californianus* Conrad
106. *Mitella polymerus* (Sowerby)
107. *Pisaster ochraceus* (Brandt)
108. *Balanus glandulus* (Darwin)
109. *Styela montereyensis* (Dall)
110. *Haliotis kamtschatkana* Jones
111. *Strongylocentrotus drobachiensis* (Müller)
112. *Strongylocentrotus purpuratus* (Stimpson)
113. *Strongylocentrotus franciscanus* (Agassiz)
114. *Mytilus edulis* Linnaeus
115. *Littorina planaxis* Phillippi
116. *Dictyoneurum californicum* Ruprecht
117. *Phyllospadix scouleri* Hooker
118. *Zostera marina* L. var. *marina*
119. *Balanus nubilus* Darwin
120. *Ulva latissima* L.
121. *Rhizoclonium riparium* (Roth) Harvey
122. *Porphyrella gardneri* Smith et Hollenberg
123. *Desmarestia ligulata* (Lightfoot) Lamouroux
124. *Amplisiphonia pacifica* Hollenberg
125. *Rhodymenia pertusa* (Postels et Ruprecht) J. Agardh
126. *Pterochondria woodii* (Harvey) Hollenberg

mopolitan in their distribution, particularly in their tolerance to extreme dilution. Extending throughout the Strait (Fig. 49) are forms such as *Alaria tenuifolia* Setchell f. *tenuifolia, Cymathere triplicata* (P. and R.) J. Ag., *Costaria costata* (Turn.) Saunders, *C. mertensii* J. Ag., *Laminaria saccharina* (L.) Lamour. f. *saccharina, Nereocystis luetkeana* (Mert.) P. and R., *Porphyra perforata* J. Ag. f. *perforata, Rhodomela larix* (Turn.) C. Ag., *Odonthalia floccosa* (Esper) Falk., *Mytilus edulis* Linnaeus, *Littorina planaxis* Philippi, and *Strongylocentrotus drobachiensis* (Müller).

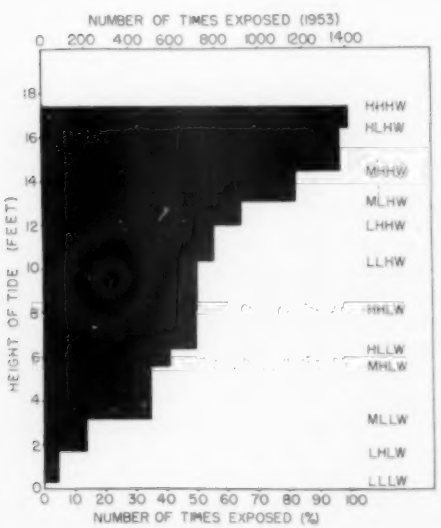

FIG. 44. Diagram showing number (and per cent) of times tidal condition caused exposure of various regions in the intertidal zone.

Restricted to the region of highest salinity, as at Hope I., are *Postelsia palmaeformis* Rupr., *Lessoniopsis littoralis* (Farl. and Setch.) Reinke, *Laminaria setchellii* Silva, *Pelvetiopsis limitata* (Setchell) Gardner f. *limitata, Dilsea californica* (J. Ag.) O. Kuntze, *Erythrophyllum delesserioides* J. Ag., *Iridaea lineare* (S. and G.) Kylin, *Hymenena setchellii* Gardner, *Ptilota asplenioides* (Esper) C. Ag., *P. californica* Rupr., *P. hypnoides* Harvey, *Mitella polymerus* (Sowerby), and *Flustrella corniculata* (Smitt).

A smooth form of *Hedophyllum sessile* (C. Ag.) Setch., *Pleurophycus gardneri* Setch. and Gardner, and *Styela montereyensis* Dall are also present in regions of highest salinity, but are somewhat less restricted in their distribution and extend into the Strait as far as Deer I.

A few organisms extend still farther into the Strait but only slightly beyond Deer I. Among these are *Alaria nana* Schrader and *A. marginata* P. and R. Still others extend from Hope I. throughout the Deer I. region and as far as Malcolm I., but not as far as the east and north sides of the Strait. Among these are *Mytilus californianus* Conrad, *Strongylocentrotus purpuratus* (Stimpson), *Macrocystis integrifolia* Bory, *Egregia menziesii* (Turner) Aresch. subsp. *menziesii*, the typical bullate form of *Hedophyllum sessile* (C. Ag.) Setch., *Alaria valida*

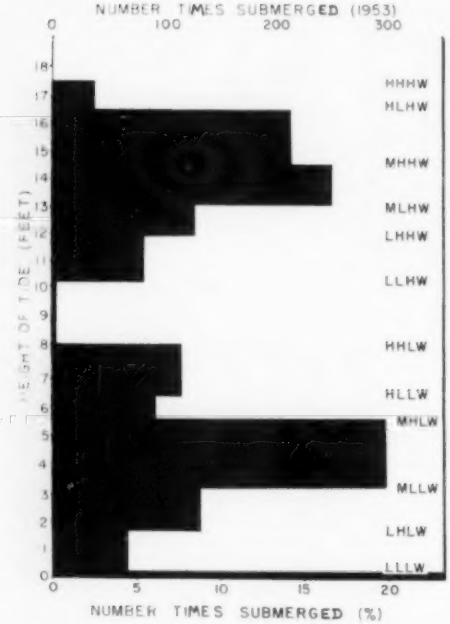

FIG. 45. Diagram showing number (and per cent) of times tidal condition caused submergence of various regions in the intertidal zone.

(Kjellm. and Setch.) f. *valida*, *Constantinea simplex* Setch., and *Haliotis kamtschatkana* Jones. Isolated populations of the abalone (*Haliotis kamtchatkana*), which have been noted farther eastward in Johnstone Strait and which may be related to local oceanographic features, present something of an anomaly in the general distribution. An exception to the general distribution described in this group is that of *Macrocystis integrifolia*. Although *Macrocystis* occurs in regions of high salinity and extends as far down the Strait as the north side of Malcolm I. and the south side of Numas I., it does not occur in the most exposed areas where *Postelsia* and *Mitella* are encountered.

Vertical Distribution of Organisms

The vertical distributions with reference to tide levels, based on data obtained using an Abney level, are presented for some of the more conspicuous organisms at Hope I. (Fig. 50). Comparisons are made also for some of these (Fig. 51) at Hope I., Deer I., and near the Klucksiwi River, to indicate the effect exposure to surf has on the vertical distribution of some organisms.

By comparing the vertical distributions of organisms in Queen Charlotte Strait (Fig. 50) with tidal data presented with respect to emergence and submergence (Figs. 42–45), a number of limiting levels are fairly apparent. Near the top of the intertidal zone is a region (HHHW to HLHW) which is rarely submerged (Fig. 43) for more than a few hours on each of a few days at any period of the year and which

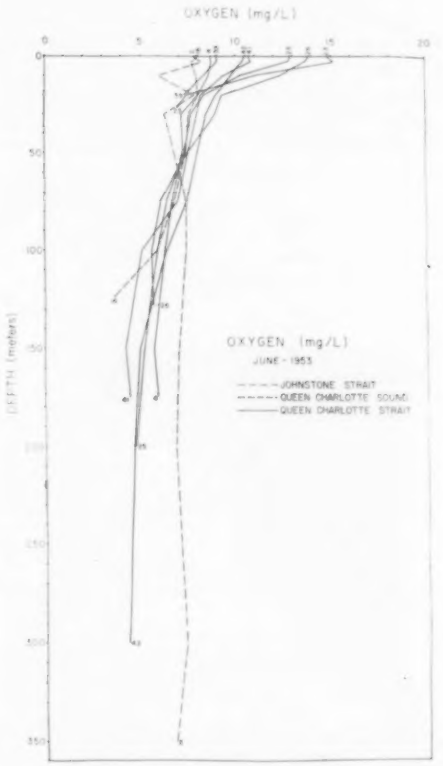

FIG. 46. Distribution of oxygen with depth at various stations in Queen Charlotte Strait and adjacent regions in June, 1953.

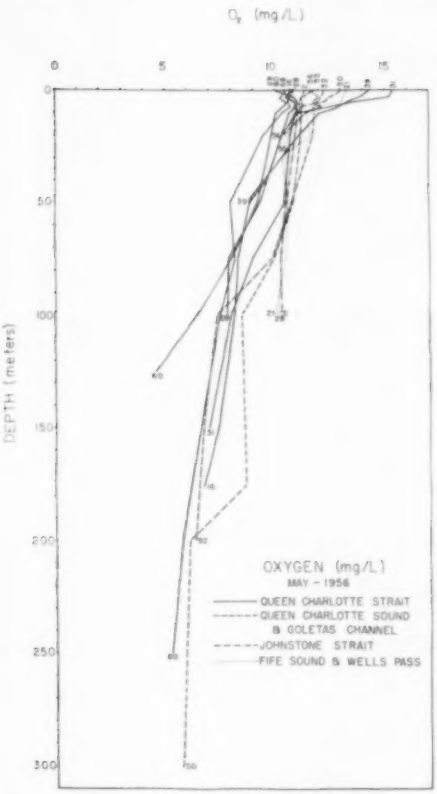

FIG. 47. Distribution of oxygen with depth at various stations in Queen Charlotte Strait and adjacent regions in May, 1956.

may be continuously exposed for as long as 4 months during the summer period. Those organisms that can tolerate such conditions are rare and in this zone one finds chiefly *Littorina,* which is capable of moving sufficiently to extend into lower less extreme zones when necessary. In the region below (HLHW to MHHW), continuous exposure to the air may last for periods ranging from a few days to almost 2 weeks, and these periods occur at least twice a month, but the rest of the time this zone is submerged at least once a day. In the region below (MHHW to MLHW), continuous exposure to the air is rarely for more than a few days at a time, and for a few months during the winter the region is submerged at least once a day. Although the upper limit of a number of the organisms (Fig. 50) in this region of the intertidal zone between 13.1 and 17.4 ft. varies to some extent with the organism, it is apparent that in this general region an upper boundary is probably determined directly or indirectly by the degree of exposure to climatic conditions. The precise tide level, if there is one, at which this boundary occurs is not clear from the data available. The effect of surf in the exposed environment may also cause some variation in the upper limit of the vertical distribution. Since the greatest change in degree of exposure within this upper region (13.1–17.4 ft.) occurs between MLHW and MHHW, a critical level is suggested at this point for a considerable number of conspicuous organisms.

All portions of the intertidal zone below MLHW are submerged at least once a day for various periods. The greatest change in conditions of submergence (Fig. 45) in the region of the middle intertidal zone (8.2–13.1 ft.) occurs between HHLW and LLHW, and it is at this point where another critical level is suggested, in some instances as the upper limit and in others as near the lower limit of the vertical distribution of certain organisms (Fig. 50).

In the lower intertidal zone (0–8.2 ft.) the most extreme change in conditions of exposure (Fig. 44) and submergence (Fig. 45) occurs between MLLW and MHLW, and this is again reflected both at the upper and lower limits in the vertical distribution of certain organisms (Fig. 50). Another critical level (Fig. 50) occurs in the region between LLLW and LHLW, where another region of marked change (Fig. 45) exists in conditions of submergence.

Although the upper limits in most instances appear to be relatively sharp, there is less consistency in this respect concerning lower limits. This suggests that other factors, perhaps competition for space or predation, may be responsible for limiting distribution, particularly downward in some instances.

DISCUSSION

Knowing as we do from experimental work the responses of some organisms to environmental factors, it seems reasonable to anticipate

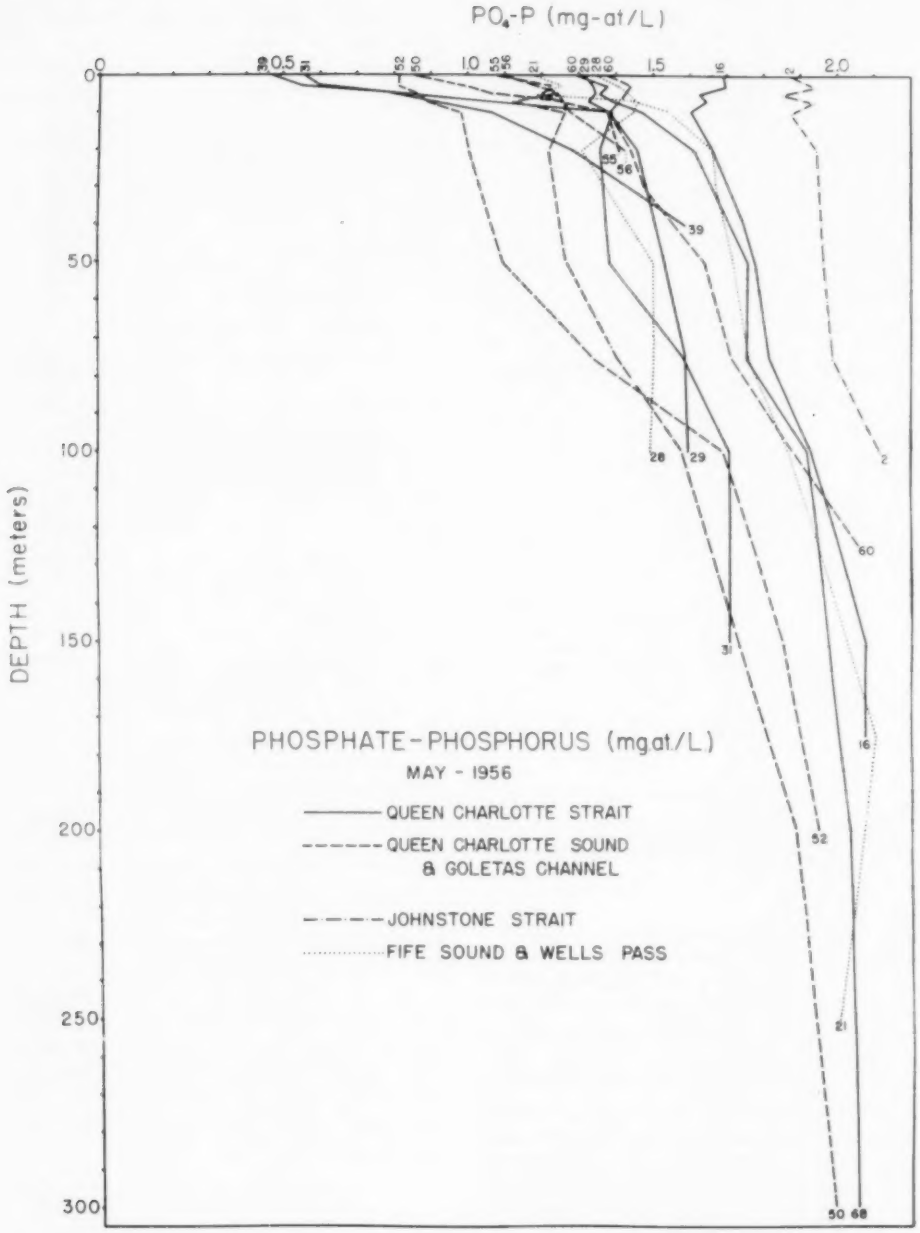

FIG. 48. Distribution with depth of phosphate-phosphorous at various stations in Queen Charlotte Strait and adjacent regions in May, 1956.

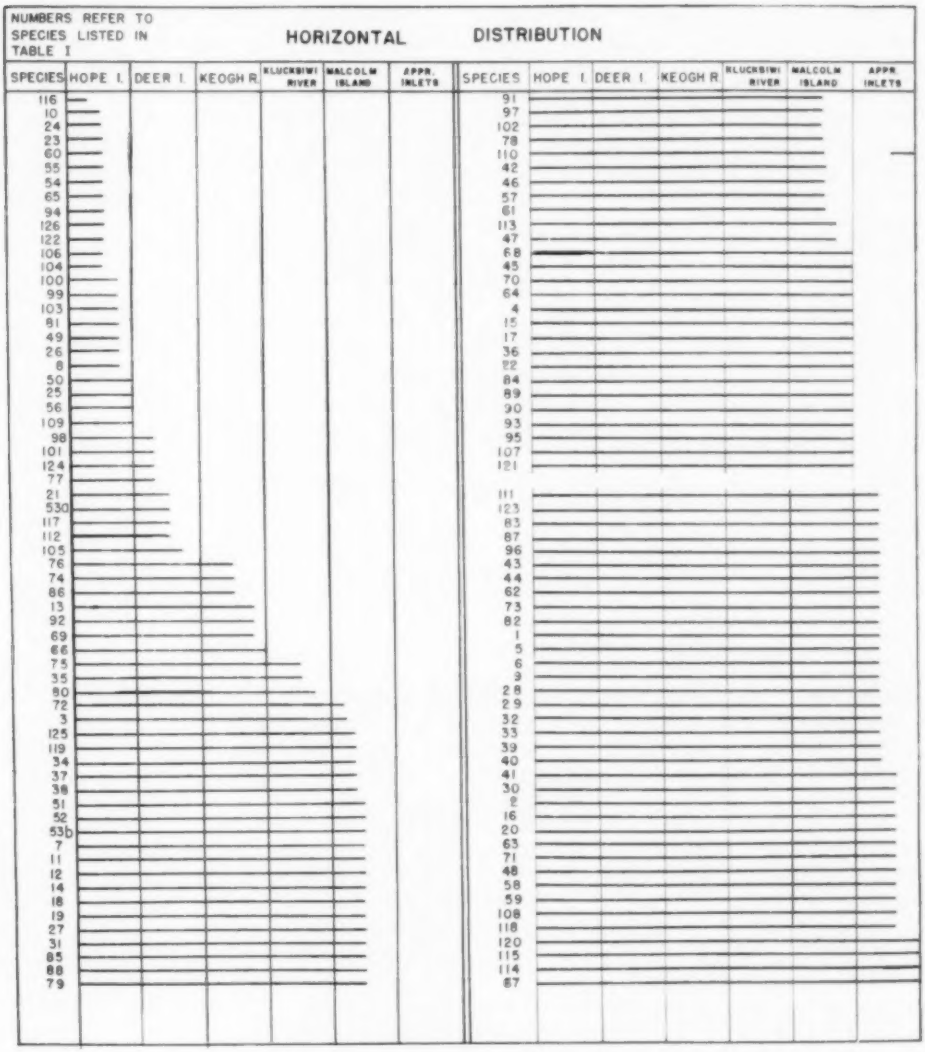

FIG. 49. Horizontal distribution of marine benthonic organisms in Queen Charlotte Strait.

that the distribution of marine organisms in time and space can be explained on the basis of oceanographic features—provided the geological, physical, chemical, and biological factors of the environment and their interaction can be adequately assessed. Any attempt to oversimplify such a many-sided and complicated study would be an avoidance of reality. However, in such a study one expects to make assumptions based on the knowledge available, in some instances of necessity by extrapolation, and to pass through a descriptive phase in an attempt to

correlate observed distributions on the basis of and in relation to other factors in the environment. These comparisons may be largely qualitative in the first instance, but the intent is that they be not only qualitative but also quantitative in the final analysis and, as in all branches of science, eventually permit predictions. At best, however, only a descriptive treatment can be attempted at this point and can only point the way to further studies and hypotheses.

There have been many attempts to describe the zonation of marine organisms on the shore, and a great jumble of appalling confusion in ecological terminology has evolved to the point where some magic significance is sometimes associated with the terms and units involved. Although the need for this descriptive phase of the study (with a minimum of terminology) is recognized at an early stage of study or in a new area under investigation, once it has served

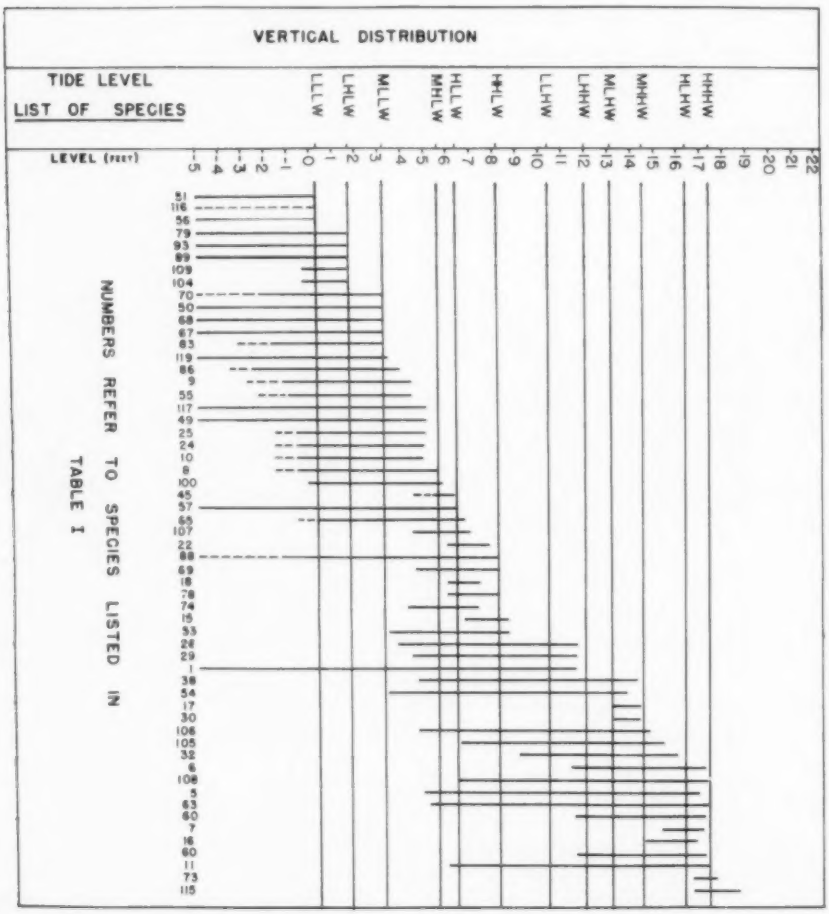

FIG. 50. Vertical distribution of some marine benthonic organisms at Hope Island.

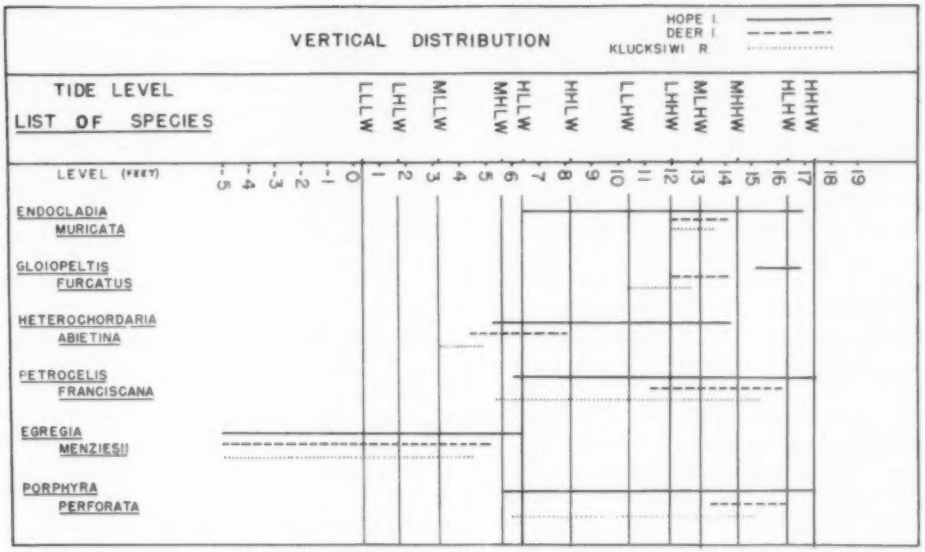

FIG. 51. Comparison of vertical distribution of some benthonic organisms at several points in Queen Charlotte Strait.

its initial purpose little refinement in this method of approach seems conducive to an explanation of the causal factors. From this point it becomes necessary to look at the problem from a new perspective involving a detailed study of the organisms concerned—an understanding of their life histories, rate of growth, reproduction, and various physiological requirements and tolerances in relation to the environment. These problems may be and, as already indicated, have been approached to some extent by actual field studies and experiments as well as by laboratory studies under controlled conditions.

It is with this philosophy in mind that this study has been approached to the extent possible from the existing data, initially from the standpoint of the oceanographer with an analysis of the environmental factors and their relation to the organisms. The success of these preliminary efforts both in the field as well as in the laboratory supports the conviction that the approach is a useful and instructive one. Differences which sometimes appear striking or significant on a broad scale are frequently less apparent and confused in a local area. The distribution of the genus *Macrocystis* is an interesting case in point. Although the global pattern of distribution of this genus is rather clearly established (Setchell, 1932; Womersley, 1954) on the basis of temperature distributions and hence follows the pattern of distribution of some of the cold water currents of both southern and northern hemispheres, the distribution of *M. integrifolia* in British Columbia follows a distinct salinity distribution. As yet, however, it cannot be conclusively stated in the latter instance that salinity itself is the causal factor. It still remains to be established whether salinity in terms of an osmotic relationship, or some parallel factor associated with open ocean water of high salinity, provides a causal mechanism for the distribution of *M. integrifolia* on this coast.

It is clear that there is a horizontal distribution of organisms, including *Macrocystis integrifolia,* in Queen Charlotte Strait which follows closely the pattern of salinity distribution in the

Strait. In turn this reflects the circulation within the area. It would be premature to say that salinity is directly responsible for the observed distributions of all the organisms encountered. But one may say that the distribution reflects the dependence on high salinity water which is characteristic of the open ocean and exposure. In some instances it may be salinity that is a direct causal factor. On the other hand, the open coast has organisms associated with surf conditions. It has been suggested that the high oxygen requirement of certain organisms is met only in such an exposed environment. However, the distributions and concentrations of oxygen in the sea in this area do not directly support this argument. The oxygen content of the waters within the sheltered Strait is as high or higher than in the surf in the exposed regions. This is particularly true in the central part of the Strait when there is a heavy bloom of phytoplankton, at which time the water may be supersaturated with oxygen to as much as 175 per cent. Likewise, although it is known that many marine algae have a high inorganic phosphate requirement, there is no evidence that this nutrient is ever limiting in this area within the zone occupied by the benthonic algae. There is a great need for further knowledge of the presence, distribution, amounts, and availability of many more dissolved inorganic as well as organic substances and perhaps even of growth substances. There is also need for a study of the quantitative aspects of removal, the rate of removal of such substances, and precise requirements for growth and reproduction in the micro-environment of the marine benthonic algae. The restriction of certain organisms to surf conditions suggests that constant movement of water is required to provide nutrients and gases which may be rapidly exhausted from the immediate or micro-environment of the individual fixed alga, or in the case of the sessile marine invertebrates, such as *Mitella polymerus*, to provide particulate food. It may be that lowering the concentration or removal by dilution or by water movement of some toxic substances which may accumulate above a certain concentration in the micro-environment is just as significant as the availability of others.

SUMMARY

A detailed study of the horizontal and vertical distributions of marine benthonic organisms in Queen Charlotte Strait has been limited so far to the more conspicuous algae and invertebrates encountered. The relationship of these distributions to the salinity distribution indicates that more intensive study of the flora and fauna in this area, as well as elsewhere on the coast, will provide further supporting evidence indicating not only the effect of oceanographic variables on the distribution and production of marine benthonic organisms but also the possibility of using such organisms as indicators of oceanographic conditions both in time and space. The relationship of the vertical distribution of some of the organisms to certain tide levels indicates the response of the different organisms to varying degrees of exposure and submergence.

This oceanographic approach, both qualitatively and quantitatively, has given a broad understanding of some of the possible factors which are likely to be responsible for the observed distributions. However, before there can be a clear understanding and explanation of the fundamental relationships between the organisms and their environment in this region, as well as an understanding of the interrelationships and interaction among the organisms themselves, additional field observations, field experiments, and laboratory experiments must be undertaken.

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Description of a New Species of *Pranesus* (Atherinidae: Pisces) from the Capricorn Group, Great Barrier Reef

D. J. WOODLAND[1]

DURING 1956–7 Richard J. Slack-Smith, Department of Zoology, University of Queensland, and the author investigated the fish fauna of Heron Island, Capricorn Group. A check list of the recorded species is to be published conjointly (Pap. Dep. Zool. Univ. Qd.). The fish described here is one of a number of new species collected at the island.

SUBFAMILY TAENIOMEMBRADINAE Schultz

GENUS *Pranesus* Whitley

Pranesus capricornensis, sp. nov.

HOLOTYPE: 93 mm. standard length, from reef flat, Heron I., Aug. 1956, collected by R. J. Slack-Smith, Queensland Museum no. I/8201.

PARATYPES: Queensland Museum nos. I/8202–5; 4 specimens, 69, 78, 85, and 88 mm.; 85 and 88 mm. fish taken along with holotype, 69 and 78 mm. fish collected by Woodland, Mar. 1957, reef flat, Heron I.

DESCRIPTION: Dorsal rays VII (V–VII) I,i,8 (9); anal I,i,12 (to 14); pectoral I,i,15; ventral I,5; caudal i,8 + 7,i. Scales from upper limit of gill opening to root of caudal fin 47 (46); median predorsal scales 21 (20); scales from origin of first dorsal to midline of belly 6½. Gill rakers on first right gill arch 5 (6) + 1 + 19 (to 22).

Depth 5.0 (4.8–5.1); head 4.2 (4.0–4.2); snout to first dorsal origin 1.75, to centre of anus 1.9, to anal origin 1.5 (1.4); all in standard length. Snout 4.5 (4.2–4.6); eye 2.4 (2.2–2.4); tip of snout to rear of maxilla 2.8 (to 3.2); least depth of caudal peduncle 3.2 (to 3.4); postorbital length of head 2.2 (2.1–2.3); distance between dorsal origins 1.5 (1.4); length of longest ray of pectoral fin 1.3 (1.2); interorbital space 2.8 (2.6–2.8); all in length of head. Least depth of caudal peduncle in its length 2.4 (2.0–2.4). Lateral band broad, its greatest width 1.5 in postorbital length of head (counts and measurements from holotype, with ranges exhibited in the four paratypes included in brackets).

Premaxilla with front margin slightly convex; teeth minute on dentary, vomer, and palatines, on premaxilla giving a shagreen-like finish to outer surface; air bladder and body cavity ending bluntly in front of anal origin; bony edge of preopercle with concavity near lower posterior corner; gill rakers long and slender, longest ⅓ as long again as diameter of pupil; maxilla reaching to halfway between vertical lines through anterior margins of orbit and pupil; centre of anus posterior to tips of depressed ventrals, 1.5 vertical scale rows distant from tips; vertical line through anus passing through fourth scale in front of first dorsal origin; anal fin origin under third scale in front of second dorsal origin; posterior margins of scales smooth; ascending premaxillary process short, broad based, not entering interorbital space (Fig. 1*a*); mandible without an abrupt elevation posteriorly on each ramus (Fig. 1*b*).

The sequence employed in listing descriptive characters is after Schultz *et al.* (1953). The formula for recording fin counts is that now in use in many taxonomic works: upper case Roman numerals for spines or, as in this instance, nonstriated rays; lower case Roman numerals for striated, unbranched rays; and Arabic numerals for branched rays.

DIAGNOSIS: *P. capricornensis* cannot be distinguished from its congeners on any single feature. Combination of the following characters is diagnostic: the broad lateral band; the scale row count from upper limit of gill opening to caudal fin base; and the position of the anus relative to the tips of the depressed ventrals and first dorsal fin origin.

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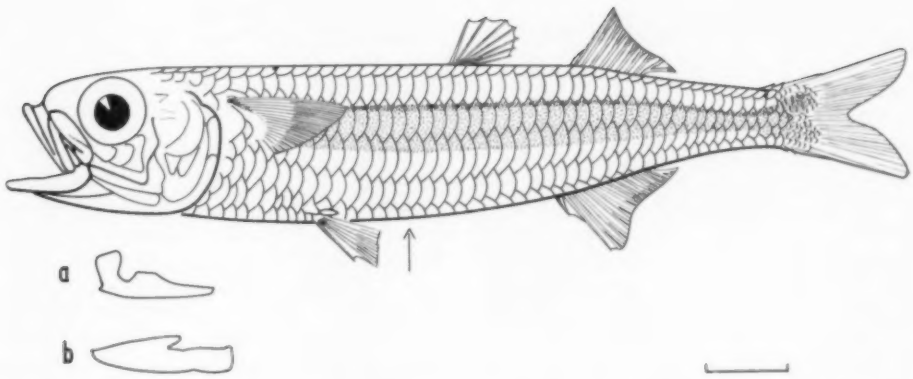

FIG. 1. *Pranesus capricornensis*, sp. nov., holotype, Queensland Museum no. I/8201 (scale line equals 10 mm.). *a*. Premaxilla; *b*. mandible.

COLOUR IN LIFE: Above lateral band, greenish; below band, silvery; lateral band silvery, but distinguishable from silver of belly by its more intense mirror-like finish; running from dorsal edge of pectoral base the full length of the upper limit of the lateral band a narrow (5.0 in width of lateral band) intense blue band terminating at root of caudal fin; a small blue spot on upper half of caudal fin scaly sheath; bluish crescent along upper ⅔ of base of pectorals; dorsals, caudal, and distal half of pectoral fins faintly dusky, other fins pale; peritoneum black.

COLOUR IN FORMALIN: Above lateral band, area lying under margin of each scale with dark pigmentation; lateral band black with a suggestion of the blue of the narrow band in its upper limits; area below lateral band pale; scaly sheath at base of caudal fin with two dark patches derived by anastomosing of lateral band; narrow bluish crescent on pectoral base persisting; colour of fins as in life.

ECOLOGY: Heron I. is a coral atoll 50 mi. from the Australian mainland (23° 27′ S., 151° 57′ E.). In the cooler months (Mar.–Aug.) immense schools of atherinids are common over the reef flat when it is flooded at high tide. All individuals taken from these schools proved to be a new species (*P. capricornensis*).

This fish was always seen swimming at depths of 1–3 ft. At low tides and during the warmer months it probably lives in open waters. The little tuna, *Euthynnus alleteratus affinis* (Cantor), which normally restricts its movement to open water, will venture on to the reef flat to feed on *P. capricornensis*.

Examination of alimentary canals of two adult fishes revealed various planktonic Crustacea, but the bulk of ingested material was unidentifiable. Females in spawning condition were recorded in Aug. 1956.

ACKNOWLEDGMENT: I would like to thank Richard J. Slack-Smith for donating specimens.

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New Pogonophora from the Eastern Pacific Ocean

OLGA HARTMAN[1]

CONTINUING SURVEYS, since 1955, of faunas in offshore areas of southern California, conducted by the Allan Hancock Foundation, using the facilities of the M/V "Velero IV," have resulted in finds of several representatives of pogonophorans. One, belonging to the genus *Siboglinum* Caullery, is believed to represent an undescribed species. Other kinds, from different places, are briefly reported below, to indicate the wide range of occurrences in deep ocean bottoms off southern California. All come from depths exceeding 950 m. and in latitudes south of 33° N. The much larger and far better explored shallower depths have yielded none, despite the examination of thousands of grab samples from shelf, slope, basin, and canyon depths of the shelf lands between Point Conception, California, to south of the Mexican border.

All specimens are deposited in the collections of the Allan Hancock Foundation. I am indebted to the Administration of the Foundation for permission and time to study these interesting materials. The cost of collecting the materials was defrayed by funds from the National Science Foundation and the Allan Hancock Foundation. Captain G. Allan Hancock has generously provided for any deficiencies in the running costs of the ship. The scientific and operating crews of the "Velero IV" took and processed the collections. Dr. Gösta Jägersten, Uppsala, Sweden, examined specimens and verified their generic affinities. The illustrations were prepared by Anker Petersen. I am indebted to all of these people for their help and interest.

GENUS *Siboglinum* Caullery, 1914

TYPE *S. weberi* Caullery, 1944

Siboglinum veleronis, new species
Figs. 1–9

COLLECTION: More than 100 specimens were taken by the "Velero IV," sta. 7049, May 7, 1960, 14.85 mi. 264° true from Point La Jolla, 32° 49′ 37″ N., 117° 35′ 12″ W., in 976 m., from the axis of La Jolla canyon near its convergence with the San Diego trench. The Campbell grab, weighing about 900 lb. with a capacity of about 5 cu. ft., recovered 2.51 cu. ft. of gray sand and green mud. In addition to the *Siboglinum* specimens, the sample yielded the kinds and numbers of animals listed below.

DIAGNOSIS: Individual tubes measure 50–65 mm. long by 0.13 mm. across. Others are longer or narrower, having a length-to-width ratio of 450–720 to 1. Each tube is usually slender, cylindrical, pale to dark straw-colored, and crossed by alternating dark brown and pale bands. The brown ones are typically paired (Fig. 2), so that both of a pair are nearly twice as long as one pale band. An occasional irregularity in this pattern results when the two dark ones are so close together as to appear fused, or are incomplete on one side to form a broader than usual, incomplete, pale band. The greater length of the tube is crossed by these alternating cross bars; only the distal anterior and posterior ends (Fig. 1) are pale and usually collapsed. The animal within lies usually some distance within the banded region; none has been found partly or wholly out of the tube. With the aid of a stereoscopic microscope the specimen can be seen through the wall of the tube and oriented with respect to the anterior and posterior regions, the tentacle in front directed forward, and the annular or uncinial band marking the approximate middle region of the body. However, dissection is necessary to study the animal more completely. Slitting the tube lengthwise has been found least destructive to the soft-bodied specimen; by using a razor-sharp, finely pointed knife and inserting it into the distal end of the tube, then extending the cut lengthwise for the length of the contained individual, one can then lift it out intact from the shell of the tube.

An entire animal measures 15 mm. long to the annular, or uncinial, region which is near the middle, making the total length about 30

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mm. The body is nearly uniform in width but is widest in the mesosomal region where it measures 0.065 mm.; the postannular region gradually becomes slenderer and tapers posteriorly. The tentacle is less than half as wide as the body and extends forward for a length nearly two and a half times that of the mesosomal length. Its insertion marks the ventral side of the body as herein interpreted, as well as the posterior end of the first body region or protosoma. The three body regions are not sharply separated from one another. The separation between the first and second regions is behind the tentacular insertion and is vaguely indicated by a faint line extending obliquely forward around the body to the middorsum. The second region, or mesosoma, is about four times longer and is separated from the third region, or metasoma, by a transverse groove located just in front of the paired glandular papillae (see Figs. 5, 6). The third region is much the longest and comprises most of the length of the body.

The tentacle is extended forward nearly straight in some specimens and is loosely to closely coiled in others, or only a short distal end is coiled. Most of the length has lateral, filiform branches or pinnules, inserted in two nearly regular rows along the ventrolateral edge (Fig. 4); those nearer the distal end are more dispersed, whereas those nearer the base (Fig. 3) are closer together and tend to be curled toward the midventral line. Each pinnule is very slender and longer than the tentacle is thick. These features agree with those described for other species of the genus having pinnules; only two (*S. inermis* Ivanov and *S. atlanticum* Southward and Southward) are said to lack them.

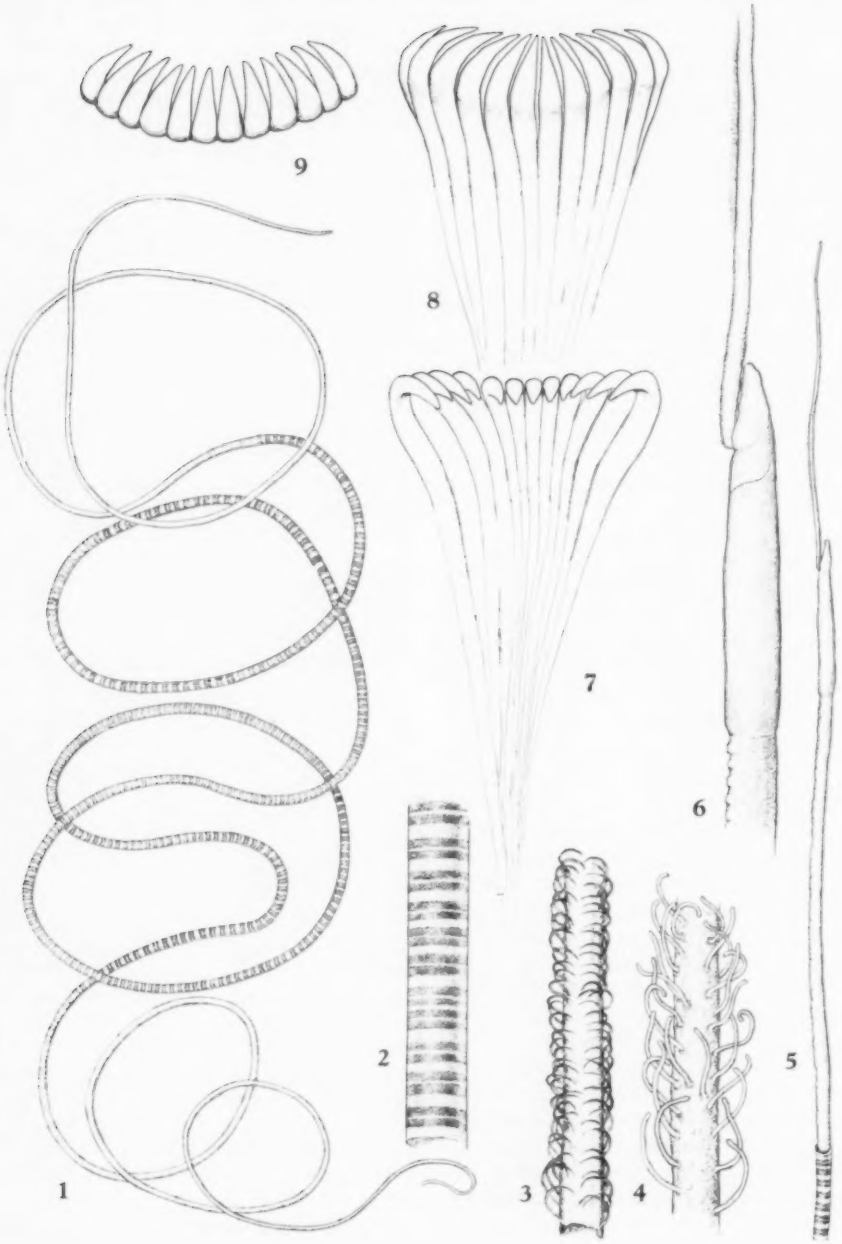
The protosoma or anteriormost region of the body is short, subconical, tapers forward, and lacks markings; its posterior end is indicated on the ventral side of the body by the insertion of the tentacle. This fusion is firm, so that the two are not easily severed. A mouth, if present, would be expected at the posterior base of this tentacle, for which the principal function seems to be that of food gathering. I have seen no oral aperture or any indication of an alimentary tube but would not exclude the possibility of a lengthwise transport tube of some kind in an animal of such great length.

The second body region, the mesosoma, is considerably longer than the first and is cylindrical in shape; near its anterior end it is obliquely crossed by the bridle or frenulum (Ivanov) or girdle (some other authors). It is separated from the third region, or metasoma, by a transverse groove. A pair of circular pores is located at the sides, just behind the frenulum (Fig. 6); they are believed to be the external apertures of the coelomoducts for the second segment.

The anterior end of the metasoma is characterized by the presence of ventrolateral paired glandular papillae; they are so arranged that the two members of a pair are separated from successive ones by a space about equal to that of the distance between the brown bars on the tube. It thus seems obvious that these papillar glands are directly concerned with tube secretion. This region is followed by the much longer goniadial region, characterized by sparsely and irregularly dispersed epithelial papillae. About halfway along the length of the body two transverse series of uncinial rows indicate the position of the annular region; for this reason the goniadial region in front is called the preannular, and the same one behind is the postannular, region.

The annulae are of particular interest because they bear hard, chitinized platelets, or unicini, in transverse series. Those of the anterior row are incomplete and number about 38, while those in the posterior row are more numerous, numbering about 44. All uncini are of one kind, and terminate distally in a single row of denticles (Fig. 8), numbering 9–13. Each uncinus is distally recurved so that those of successive uncini tend to overlap. Seen from the end the denticles form an arcuate row (Fig. 9). The basal or embedded stems are not chitinized but taper rapidly to very tenuous strands, and are so prolonged that all those of one transverse series are brought together as a fascicle and carried obliquely forward to attach to the body wall. They may function to anchor the animal within the tube at selected places. The comparable uncini in some other species, *S. atlanticum* and *S. inermis*, have been shown as having multiple rows of crenulations (see Southward and Southward, 1958: 629, 631).

S. veleronis was recovered from a quantitative sample covering a surface area less than a half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a square meter. The animals contained in the mud, without tubes, weighed about 6.4 g. (moist weight). They included the following:

Siliceous sponge spicules, scattered through the debris
Anemone, small white, 1
Crustaceans (not identified)
ostracod, 1; amphipod, 1; cumacean, 2; gnathid isopod, 2
Mollusks: more than 100 living small gastropods, pelecypods, and 3 small solenogasters (not identified)
Echinoderms, identified by Fred Ziesenhenne
Ophiacantha normani Lyman, 2
Ophiura kofoidi J. F. McClendon, 22
Polychaetes: with 22 species and more than 200 specimens
Ancistrosyllis tentaculata Treadwell, 3
Axiothella sp., 6
Aricidea aciculata Hartman, 3
A. uschakowi Zachs, 32
ampharetid, juveniles, 4
Brada glabra Hartman, 12
Chaetozone ?gracilis (Moore), 2
Chaetozone sp., fragments, 2
Cossura candida Hartman, juveniles, 2
Glycera ?capitata Oersted, juveniles, 2
Haploscoloplos elongatus (Johnson), 4
Heteromastus ?filobranchus Berkeley, 4
Maldane cristata Treadwell, 13 (the largest and most conspicuous in the sample, contained in thick, mudwalled tubes with lateral vents and branches)
Myriochele ?gracilis Hartman, juvenile, 1
Ninoe fusca Moore, 12
Nothria sp., juvenile, 1
Paraonis gracilis oculata Hartman, 77+
Pilargis hamata Hartman, 1
sabellid tube, 1
Terebellides sp., juvenile, 1
Tharyx monilaris Hartman, 10+
T. tesselata Hartman, 4
Pogonophora
Siboglinum veleronis, new species, 100+

The total number of species and specimens is thus 30+ and 428+.

SYSTEMATIC AFFINITIES: *S. veleronis*, the eleventh species to be described in the genus *Siboglinum*, differs from others in that the tube has double bands of dark brown bars, and the uncini of the annular region have 9–13 teeth in a single transverse row. The proportional lengths of the first and second body regions, shown in Figures 5 and 6, differ from those of other species.

It is noteworthy that all but two of the known species occur in far northern latitudes. Six come from the northwestern end of the Pacific Ocean; three others are from the northeastern part of the Atlantic. The first species of the genus, *S. weberi* Caullery, came from the Malay trench in great depths, and the present species is the first to be described from the western hemisphere. These species, with their distributions are as follows:

S. weberi Caullery, 1944, IndoPacific area, in 462–2060 m., in fine sand and mud.

S. ekmani Jägersten, 1956, Skagerack, northwestern Europe, in 487–650 m., clay.

S. caulleryi Ivanov, 1957, Ochotsk Sea, in 90–200 m., and other northwestern Pacific areas in depths of 23–8100 m., in the Kurile trench.

S. cinctulum Ivanov, 1957, northwest Pacific, in 3420 m., in the Kurile trench.

S. pellucidum Ivanov, 1957, southwestern part of the Bering Sea in 1740–4820 m.

S. minutum Ivanov, 1957, Bering Sea in 3740–3840 m., and Kurile-Kamchatka trench in 5540 m.

S. fedotovi Ivanov, 1957, southwestern part of the Bering Sea in 3330–3940 m.

S. plumosum Ivanov, 1957, Ochotsk Sea east of Japan, in 124–318 m.

FIGS. 1–9: *Siboglinum veleronis*, new species, from "Velero IV" sta. 7049. 1, Entire tube containing animal, × 22; 2, part of tube showing paired dark alternating with pale bands, × 89; 3, part of tentacle from near base, showing pinnules curled toward midventrum, × 228; 4, another part of tentacle from another individual, with pinnules nearer tip of tentacle, × 228; 5, animal with tube partly dissected away, tentacle directed forward, in left lateral view, × 25.5; 6, enlarged anterior regions including protosoma, mesosoma with frenulum and pore of coelomoduct, and part of glandular metasoma, in left lateral view, × 83; 7, an uncinus from annular zone, seen from denticled side, × 5,720; 8, an uncinus seen from opposite side, × 5,720; 9, an uncinus seen from top, showing arcuate arrangement of denticles, × 5,720.

S. atlanticum Southward and Southward, 1958, from the northeastern Atlantic, in 600–1400 m.

S. inermis Southward and Southward, 1958, from the same locality as the preceding.

S. veleronis, n. sp., from La Jolla canyon, southern California, in 976 m.

In addition to *S. veleronis,* the collections of the Allan Hancock Foundation contain representatives of three other pogonophores. One is mentioned earlier (Hartman and Barnard, 1960: 283) coming from West Cortes, East Cortes, and Long basins and from the San Diego trench. The collar segments of the tube measure 2.9 mm. across and 3.3 mm. long; each is drab dark brown, cylindrical, paler at one end where it flares and is frayed. In size and shape they most nearly resemble those shown for *Galathealinum* (Kirkegaard, 1956: 81).

Another kind, a *Siboglinum* sp., has just been received from a trawl station, "Velero IV," sta. 7231, off San Eugenio Pt., Lower California, Mexico, in 4800 m. This organism inhabits tubes which, in size and color, resemble those of *S. veleronis,* but the alternating brown bands are single, not double, and range from four to six times as long as the pale ones, or only a little longer. The protostoma has a pair of small red eyespots at the sides—the first known instance of eyes in pogonophores. The ventral side of the tentacle appears villous, due to paired rows of long, closely set pinnules. The uncini are in two transverse, single rows and are set far apart, the distance being about equal to four times that of the body width.

A fourth species is *S. ekmani* Jägersten, from the Skagerack, Denmark, a gift from the Zoological Museum at Copenhagen.

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Acanthophora, a Possible Invader of the Marine Flora of Hawaii[1]

MAXWELL S. DOTY[2]

IN THE FALL OF 1952, a small algal fragment was brought to the author from Pearl Harbor[3] by Mr. Charles Cutress. In April, 1953, a much larger piece of the alga was brought in by Mr. Spencer Tinker, who had found it washed ashore near the Waikiki Beach Laboratory of the University of Hawaii. Both collections were readily determined as representing a species of *Acanthophora* Lamouroux (1813: 132), a rhodophytan genus. This genus is distinct and clearly recognizable among the floral elements occurring in this part of the world. A search of the literature and the herbaria available revealed no Pacific records of this genus from the Hawaiian Islands or, with one exception, east of the Western Caroline and Marianas islands north of the equator.

Other collections during succeeding years, and field observations as well, revealed a huge increase in the abundance of the species in Hawaii during the next few years. In May, 1953, Dr. D. W. Strasburg found this alga "in abundance" at Keehi Lagoon, between Pearl Harbor and the Port of Honolulu on the leeward side of Oahu. Later the same month, a dense growth of the alga was found by the author (numbered 10774) and Dr. E. Y. Dawson at Hauula, north of Honolulu, on the windward side of the island of Oahu. Parts of this collection are the earliest collections from Hawaii represented in both the Bishop Museum and the University of California herbaria. From that time on, *Acanthophora* has been so common on the leeward side of Oahu that it has not often been preserved as an herbarium specimen.

Finally, during June, 1956, Dr. Otto Degener collected and sent in a specimen (his no. 24105) from Mokuleia on the windward shore of the island of Oahu, northwestward from Honolulu, collected by himself, Miss Marie Neal, and Dr. Constance Hartt, with the annotation ". . . ubiquitous some distance within the reef; observed very rare here last year. This is first time aggressive marine alga threatening native kinds." Certainly it appears to be replacing (crowding out) elements of the native flora. Degener, who has paid close attention to the reef population at this particular site, feels the alga probably was not there until, at most, 2 years before this collection was made.

Not only have frequency of observance and density of standing crop increased, but the distribution has been that of a progressive encircling of Oahu, one of the few islands of the Hawaiian Group where *Acanthophora* has been found.

The alga has spread to Kauai, another of the Hawaiian Islands. Mr. Jan Newhouse has passed on local stories that the alga was not found around Kauai until about 1954 or 1955, and the observation that it is now ubiquitous. This genus was recorded from Kauai by Kohn and Helfrich (1957: 243). Their mention of the genus was based on observations of Newhouse about November, 1956, and was not included among the algae they collected and had identified by Dawson at the time their earlier work (Helfrich and Kohn, 1955) was completed in October and November of 1955. It has been found neither among our earlier extensive collections from Kauai nor by Newhouse among his, but during August 1960, Dr. Charles Lamoureux and Mr. Tadayuki Kato made a collection (Lamoureux coll. no. 1542) of *Acanthophora* on Kauai at Poipu Beach.

Specific, though in part cursory, searches during 1960 for *Acanthophora* on the islands of

[1] This work was made possible by a research time grant from the Graduate Research Committee of the University of Hawaii and facilitated by Office of Naval Research contract 2591 (00).

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[2] Botany Department, University of Hawaii, Honolulu 14, Hawaii.

[3] According to Mr. Mikihiko Oguri, this algal collection probably came from West Loch, between Laulaunui Island and the northwestern shore.

Hawaii, Lanai, and Maui variously by Robert K. S. Lee, Mikihiko Oguri, Warren Wilson, and the author have resulted in no traces of this alga being found with one exception. The exception is a collection made by the author (numbered 19431), Mrs. Meng Sung Doty and Mr. Lee along the north shore of Lanai in November, 1960, where the alga was washed onto the muddy sand beach in abundance, free or attached to shells, coral, or even rocks up to 2 lb. in weight. Unfortunately, the Kawaihae area on Hawaii and the shores of Molokai have not been specifically searched for this genus, but our collections made during earlier years from these places do not include *Acanthophora*.

In the light of the ability and persistent vigor of the algologists who have at one time or another concerned themselves with the marine algae of the Hawaiian Islands, e.g., Drs. W. A. Setchell, Josephine Tilden, G. F. Papenfuss,[4] I. A. Abbott, and earlier, the Misses Minnie Reed and Marie Neal, and Mrs. Nina H. Loomis, it seems unlikely that this alga would have been overlooked had it been consistently present. It is a conspicuous alga. The older Polynesians in Hawaii seem to have had no name for *Acanthophora*. If pressed for a Polynesian name nowadays, the common man professing native acumen will apply local names such as manauea, the name widely used formerly for species of other genera, such as *Gracilaria* (now usually referred to by the Japanese name, ogo).

Identifying the Hawaiian alga has led to a consideration of the differences purported to exist between the several species reported in the Pacific. Many variants can be found in the material that has been available for this study from both the Atlantic and the Pacific, but for the present it is felt that the many forms found might best be treated as variants of one species. *Acanthophora spicifera*[5] (Vahl) Boergesen (1910) is the name for this species having priority insofar as we know.

Among the most common names[6] considered here as having been applied to the taxon *A. spicifera*, as found in the Pacific, is *A. orientalis* J. Agardh (1863). In describing *A. orientalis* as a new species, J. Agardh listed the Marianas Islands, of which Guam (13° N., 145° E.)[7] is one, as the source of one of the two collections he had seen. The other collection was probably from Manila Bay (14° N., 121° E.) in the Philippines. Safford (1905: 30–32) says that in the Marianas, the islands Guam, Rota (14° N., 145° E.) and Tinian (15° N., 146° E.) were visited by the Freycinet expedition. The material of this expedition from these islands is believed to be the source of one of the two collections Agardh reported. In his text, Safford (1905: 177 f.) lists *A. orientalis* from Guam and we presume this to be based on the Freycinet record, since Safford also says Dumont d'Urville collected several new species of algae on Guam. We ourselves have seen no specimens from Guam, despite a search through the several collections, now in our possession, which were made there by Mr. Ernani Meñez in 1960.

Except for the reports from Hawaii, the genus is not known to occur in the Pacific east of the Marianas other than in the Ponape region, where it has been reported by Yamada (1944: 44) as *A. muscoides* (L.) Bory from Ant (7° N., 158° E.), an atoll 8 mi. to the southwest of Ponape.

It is common about the large subcontinental or continent-related islands of the far western Pacific and, as *A. spicifera*, according to Womersley (1958), in northern Australia. The genus is reported (Kanda, 1944: 749) from Palau (7° N., 134° E.) as *A. orientalis*. As *A. thierii* Lamx. the genus is recorded from the Admiralty Islands (probably 2° S., 147° E.) and Tongatabu (21° S., 175° W.) by Dickie (1875*b*: 238, 235, resp.) and from Torres Straits (10° S., 143° E.) by Dickie (1876: 447). *Acanthophora* is common in the warmer part of the Atlantic, and Lamouroux (1813) believed the genus to be circumequatorial.

It seems entirely possible that this species

[4] In correspondence, Dr. Papenfuss tells us that neither he nor Setchell found this genus in Hawaii, and that the only Hawaiian specimens in the University of California herbarium are duplicates of the Hauula collections sent in by Dawson and mentioned above.

[5] Basonym=*Fucus spiciferus* Vahl, 1802.

[6] The only similar species not mentioned otherwise here appears to be *A. aoki* Okamura, 1934.

[7] The approximate latitude and longitude in degrees is given for the convenience of those interested in the location of the places named.

could have arrived in Hawaii from the west on a ship bottom, i.e., a man-made facilitation of the oceanic drift method of dispersal. This would be the carrying of an organism "upstream."[8] The progressive increase in abundance around the island over several years' time, and, recently, what appears to be a leveling off in abundance, is considered evidence of an introduction into the Honolulu–Pearl Harbor area. The Honolulu–Pearl Harbor shore area is the part of the state having the greatest traffic with regions of the world where *Acanthophora* has been known as a common component of the flora for a long time. This area is not climatically extreme for the state. However, since Honolulu has been in contact with the East and West via ship for centuries, it seems likely that some recent unusual occurrence may have implemented this transport. The three following events have come to our attention and are considered in this regard.

First, the recent warming of North Pacific waters (e.g., since the low temperature year of 1955 at Christmas Island, 2° N., 157° W.) would not, it seems, be accountable for the following reasons: first, the warm temperatures did not begin until after the alga was well known in Hawaii, and, secondly, there has been little abnormality of water temperatures in the Hawaiian area itself.

A second unsual event that may have led to the introduction is the increase in traffic between the Honolulu–Pearl Harbor area and the Far East during World War II, 1941–45, and during the Korean Police Action, 1950–53. The idea is that a number of small introductions at nearly the same time might have provided together a sufficiently large inoculation for the species to become established. From the rate of spread we tend to exclude the first period. The second is more timely. There is no special evidence that would lead one to choose this latter as the probable period, though such changes in oceanic traffic have been held to account for the distribution of barnacles in some cases elsewhere in the world.

A heavily fouled barge, the "Yon 146," towed to Pearl Harbor from Guam, provides an example of the third, and more specific, type of event that may have led to the establishment of *Acanthophora* in Hawaii. The idea here is that one heavily "fouled bottom" could have provided a sufficiently large inoculation for the species to become established. Upon arriving in Pearl Harbor February 3, 1950, this "fuel oil barge (nonself-propelled)" was placed in a dry dock. The Pearl Harbor dry docks are about 12 km. by water and 8 km. in a straight line from the place Cutress collected the first material of *Acanthophora* found in Hawaii. The dry dock is about 30 km. by water from the place Tinker first found this species of *Acanthophora*.

Fish and gastropod collections were made both from the growths, often 3–8 in. thick, on the barge and from the small pools left under the barge in the otherwise dry dry dock. They were made, at least in part, on April 10, 1950, and variously by Tinker, George Campbell, and Kenneth A. Wong. This vessel, 200 ft. long, 56 ft. in beam, concrete-hulled, under different descriptive names, has been mentioned as a possible means of fish introduction by several authors, e.g., by Gosline and Brock (1960: 26), who have studied collections made on it. The same vessel is reported by Edmondson (1951: 183, 212) as having brought in invertebrates which have become established,[9] such as the brachyuran crab, *Schizophrys aspere*, common to the far western Pacific. Chapman and Schultz

[8] This is the customarily postulated direction of migration in deriving the populations of Hawaii, as summarized by Zimmerman (1948), and Gosline and Brock (1960). Ladd (1960) has emphasized a somewhat different possible mode of origin for the populations of the Pacific islands.

[9] From accounts of long-time residents of the area, known distribution of the species, and information in the literature, it seems to me almost certain that *Cotylorhizoides pacificus* (Mayer) and *Cassiopea medusa* (Light), both Rhizostomae, were accidentally introduced to the Pearl Harbor area during the 1941–45 period. The type locality of these two medusae is the Philippine Islands. In Hawaii both were restricted to Pearl Harbor until about 1950. About this time, *Cassiopea* appeared in Honolulu Harbor and the Ala Wai Canal. Later, 1953–54, *Cotylorhizoides* appeared in Kaneohe Bay. Until the time of my departure (December, 1955) neither medusa was known from the other Hawaiian Islands, Line Islands, Marshalls, Gilberts, etc. Both forms undoubtedly came to Hawaii as scyphistoma on ships or the like, as neither are medusae of the open ocean.—C. E. Cutress, June, 1960.

(1952) concluded there was no evidence among the fish records they obtained that species had been brought to Hawaii in the fouling population on that barge. Dr. C. M. Burgess, who, along with Campbell and Tinker, provided much of the specific information on these events, told the author that the species of the molluscan genus *Cypraea* brought in on this vessel, the "Yon 146," did not become established in Hawaii, and this has been affirmed by Dr. Alison E. Kay, who is a student of this genus.

In commenting upon *Tripterygion hemimelas* Kner & Steindachner and *Ecsenius hawaiiensis* Chapman & Schultz, two blennioid fishes reported to have been collected from the pools of water in the dry dock holding the "Yon 146," Strasburg (1956: 245 f.) notes that the specimens of *T. hemimelas* were similar to a species from the Samoan Islands (14° S., 171° W.). The service record of this barge, as far as the author has been able to trace it, indicates that it was tied up at Apra (13° N., 145° E.), Guam, from 1945 to the date it was towed to Pearl Harbor, a period of about 4 years. Thus is does not seem likely that it would have been directly the means by which a Samoan fish would have been introduced into Hawaiian waters. Whether *T. hemimelas* occurs in Guam or not is not known to the present author.

Possibly the blennioid fish, *Omobranchus elongatus* (Peters), was brought to Hawaii (Strasburg, 1956: 257) from the Samoan area along with chunks of reef rock bearing living specimens of the giant clam, *Tridacna*. At least for the present, this splendid possible avenue of introduction is discounted; though *Acanthophora* has been reported (Reinbold, 1896) as *A. orientalis* from Upolu (14° S., 171° W.), Western Samoa.

Individual ships have been cited previously as the means by which algae have been introduced into the Central Pacific. Dickie (1875*a*: 33) published a note to the effect that *Ulva latissima* Linnaeus was introduced to Mangaia (22° S., 158° W.) in the Cook Islands when a whaling ship from the Antarctic was wrecked there on the reef in 1852. There is the possibility, however, that the wrecked ship merely provided a favorable habitat, in which habitat an ulvoid alga interpreted by Dickie as representative of this specific taxon appeared. In form the ulvoid algae, of the larger benthic algae, are among the most plastic in respect to environmental conditions.

Kohn (1959: 81) records *Acanthophora* (using the binomial *A. orientalis*) from Kaneohe Bay, Oahu, Hawaii, where it was the substratum upon which the eggs of *Conus quercinus* were found attached in February, 1956. *C. quercinus* has been recorded for Hawaii for many years (e.g., Bryan, 1915: 454), but the alga for only a few years. If *C. quercinus* is very host-specific in its egg-case depositing, this observation of Kohn's could be taken to imply long presence of *Acanthophora* in Hawaii. Though the alga is independent of the mollusc, if the mollusc is restricted to the algal species for egg-case deposition, the alga would probably have had to be here first and it would have taken many years for the mollusc to develop modified egg-case depositing habits including *Acanthophora* as a host. Our impression[10] is, however, that egg-case attachment by molluscs is not very specific, substratum-wise, and therefore, that there is no implication in Kohn's record that *Acanthophora* grew in the islands, say, in 1915.

After considering the types of events described above, we feel that it is most likely that *A. spicifera* arrived recently in Hawaii via the fouled bottom of a ship. Aside from the ordinary ship traffic, similar opportunities for introduction by vessels other than the "Yon 146" are known. One of these opportunities is provided in the case of a similar vessel, the "Yogn 41," which was towed from Subic Bay (15° N., 120° E.) in May, 1947. This "gasoline barge (non-self-propelled)" was dry-docked in February, 1950, in Pearl Harbor. While Subic Bay is unknown phycologically, *A. spicifera* is common in the general area, e.g., in Manila Bay a few miles to the south it is abundant. However, from the timing of the events and from the rate of spread after the first specimens were found, it is believed that

[10] A letter received since from Prof. J. M. Ostergaard supports this impression concerning the specificity of egg-case deposition by *Conus* and tells us of his "finds" of *C. quercinus* in the Honolulu Harbor area as dead shells in 1902 and 1905 and as living shells in 1915.

an earlier vessel would be much less likely a source of the introduction of *A. spicifera* than the "Yon 146."[11]

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[11] Though we do not know what other biological consternation may be associated with this vessel, it may cause little more for Hawaiian biologists, for it is reported to have been sunk in Subic Bay on October 16, 1955.

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Post-larval Food of the Pelagic Coelenterate, *Velella lata*

ROBERT BIERI[1]

HUGE, UNEXPECTED SWARMS of *Velella* that have drifted onto the coasts of France, England, the United States, and other countries have stimulated many of the studies on the "purple sail." Although recent reports (Savilov, 1958; Bieri, 1959) have indicated some of the reasons for the apparently haphazard appearance and disappearance of these swarms, we have little or no idea of the effect of such sporadic invasions on the local fauna. The size of these populations is indicated in several published reports, of which Woltereck's (1904) is typical. This particular swarm when cast onto the beach at Villefranche formed a mound ½ m. wide, ½ m. high, and fully 1000 m. long. Such huge populations must have a considerable effect on the community of organisms in the sea beneath them.

This paper records some quantitative data on the food of *Velella*. Some possible effects of predation by *Velella* on associated zooplankton are suggested.

MATERIAL AND METHODS

In the present study, 137 specimens were used. Ninety-nine of these were obtained by dip-net between 0915 and 1000 at 32° 41′ N., 121° 04′ W. on May 10, 1950. These specimens were sorted into five size-groups and preserved in formalin. On March 29, 1954, 38 specimens were collected in a special surface net between 1400 and 1500 at 32° 40′ N., 118° 16′ W., and were also preserved in formalin.

In the laboratory all gonozooids were cut from the specimens and examined at 12× magnification. Those parts containing visible food were removed and dissected, and the food items were identified. The main central gastrozooids were dissected separately. Details of the weight determinations are given in Bieri and Krinsley (1958).

RESULTS AND DISCUSSION

Only three brief comments on the food of *Velella* appear in the literature. Huxley (1858) found copepod remains in the gonozooids, while Lebour (1947) reported a young "macerated" *Velella* with its "stomach" (main central gastrozooid) full of harpacticoid copepods. Totten (1954) reported a calanoid copepod and crustacean remains in the gonozooids. No quantitative data are available.

In the present study most of the food was found in the gonozooids. Only 33 per cent of the specimens examined had food in the main central gastrozooids. Digestion occurs in both the gonozooids and the gastrozooid, as is evidenced by the exoskeletons of crustaceans found in both places. The food in the gastrozooid was somewhat larger on the average than that in the gonozooids. Possibly the gastrozooid ingests the organisms caught by the gonozooids that are too large for them to ingest. However, the gastrozooid also ingests small items.

In the 99 specimens taken off California in May 1950, fish eggs (mostly those of jack mackerel, *Trachurus symmetricus*[2]) made up 48 per cent of the total food by count. Euphausiid eggs made up 7 per cent of the food items. On the other hand, in 38 specimens taken off California in March 1954, euphausiid eggs made up 78 per cent of the food items and fish eggs 3 per cent by count.

The fish eggs had an average diameter of 1.1 mm., the euphausiid eggs a mean diameter of 0.41 mm. Thus a fish egg has nearly 17 times

[1] Antioch College, Yellow Springs, Ohio. The early stages of this study were carried out at the Scripps Institution of Oceanography, La Jolla, California, and the Lamont Geological Observatory, Palisades, New York. Manuscript received July 29, 1960.

[2] Dr. E. H. Ahlstrom, U. S. Fish and Wildlife Service, La Jolla, Calif., kindly identified the fish eggs.

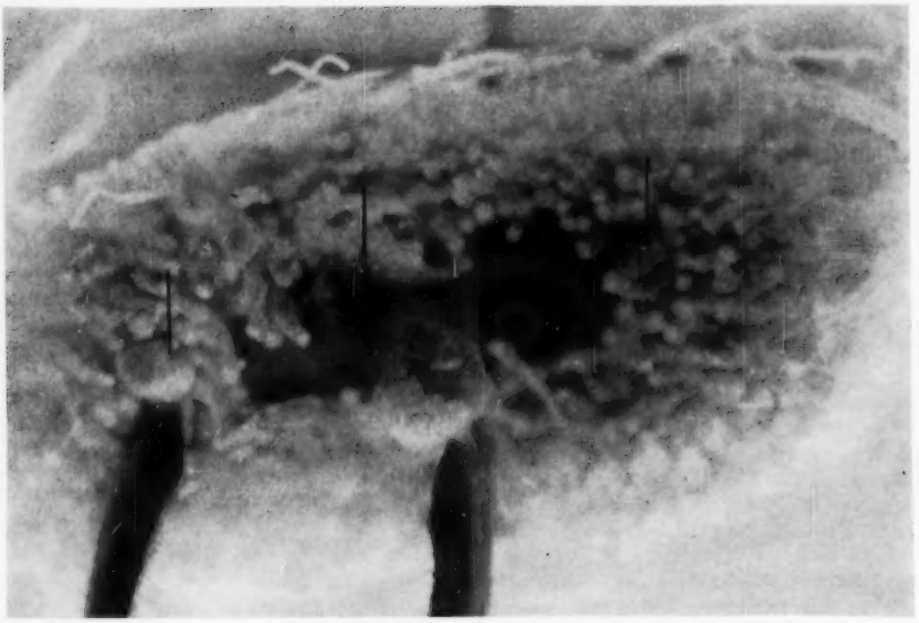

FIG. 1. Ventral side of *Velella* killed and fixed in process of eating three large and three smaller fish eggs. Smaller eggs, marked by vertical lines, have diameter of 1.1 mm. Gastrozooid surrounding central egg has broken and appears as thin film above egg. Darkest egg is not completely ingested.

the volume of a euphausiid egg. This means that in the *Velella* taken in March of 1954, fish eggs almost equalled the volume of euphausiid eggs in the diet of *Velella,* while in the May 1950 sample fish eggs were 120 times the volume of euphausiid eggs. The ventral side of a *Velella* taken in the process of eating six fish eggs is shown in Figure 1.

When the *Velella* were collected in March 1954, a surface net tow was taken at the same time. In Table 1 the per cent composition of the plankton is compared to the per cent composition of the food of *Velella.* Euphausiid metanauplii and copepods were 10 times as common in the plankton as in *Velella* food. On the other hand, euphausiid eggs were nearly 8 times as common in the food of *Velella* as in the surface zooplankton. Larvaceans, which made up 10 per cent of the food by count, formed less than 0.1 per cent of the plankton. If the plankton sample is representative of the food that was available to this particular *Velella* population (change with time or micro-vertical distribution differences may mean the plankton sample is not representative), it appears that motile organisms such as copepods and nauplii are not caught as effectively as are weaker swimming zooplankton, such as the larvaceans or the nonmotile eggs of fish and invertebrates. Nevertheless, comparatively large and active organisms such as larval fish and adult euphausiids are occasionally caught.

In Figure 2 the per cent composition by count of the food of the 99 specimens taken in May 1950 is shown as a function of mean length of *Velella.* Apparently there is no marked food selection by the different sizes of *Velella* although the calanoid copepods (3) increase steadily in importance when *Velella* surpasses a length of 30 mm. This is another indication that motile organisms are not caught as effectively as are nonmotile objects. Besides jack mackerel eggs and the items listed in Table 1, the following items were found in the gono-

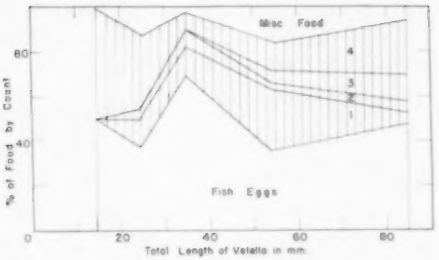

FIG. 2. Per cent composition, by count, of *Velella* food as function of total length of *Velella*. Shaded area is crustacean food. *1*, Euphausiid eggs, *2*, barnacle cyprids, *3*, calanoid copepods, *4*, other crustacean food. There appears to be no marked food selectivity by the different sizes, although copepods increase in importance in diet at sizes above 30 mm.

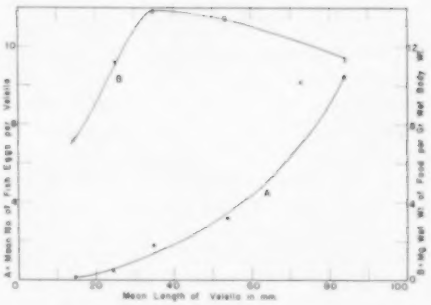

FIG. 3. Amount of food caught as function of length of *Velella*. Although number of fish eggs increases rapidly with length, weight of food caught per gram of wet body weight decreases after length of about 40 mm.

zooids and main central gastrozooids of *Velella* but were not studied quantitatively: larval fish, including a saury; chaetognaths and their eggs; barnacle nauplii, probably of *Lepas;* siphonophores; larvae of decapod Crustacea; adult mysids; copepod eggs and nauplii; larval and adult euphausiids; corycaeid copepods; pteropods. *Velella* also were found to have eaten the diatom *Coscinodiscus* and the medusae of other *Velella*. One specimen had eaten a fish scale. Specimens cast upon the beach were found to have ingested sand into the gastrozooid as well as into the gonozooids. Thus it appears that *Velella* is a carnivore, feeding on anything it can catch, generally weakly swimming or nonmotile zooplankton.

In Figure 3 the mean number of fish eggs caught by various sizes of *Velella* is shown as curve *A*. The number increases rapidly with increasing length of *Velella*.

The amount of food in each size group of *Velella* was too small to allow reliable weight determinations. Therefore, the wet weight of food present was estimated by calculating the volume of the fish eggs, assuming their density to be one, and assuming that the crustacean food on the average was one-third the weight of the fish eggs. On the basis of these assumptions, the weight of food caught per gram wet body weight of *Velella* is shown as a function of the length of *Velella* (Fig. 3, curve *B*). At lengths greater than about 40 mm. the *Velella* increase in weight more rapidly than they increase the amount of food caught.

TABLE 1

FOOD OF *Velella* COMPARED TO ASSOCIATED ZOOPLANKTON

BY COUNT	% OF *Velella* FOOD (38 specimens)	% OF PLANKTON (0–½ m. net tow)
Euphausiid eggs	78	10
Euphausiid metanauplii	0.5	52
Copepods	3	34
Anchovy eggs	3	3
Other fish eggs	0.5	<0.1
Larvacea	11	<0.1
Barnacle cyprids	0.5	<0.1
Hyperiid amphipods	0.5	<0.1
Cladocera (*Evadne*)	1.0	<0.1
Emerita larvae	1.5	<0.1
Parasitic copepods, *Caligus*	0.5	<0.1

CONCLUSIONS

The data given above indicate that *Velella* is essentially carnivorous, feeding more or less indiscriminately on zooplankton primarily within the size range 0.2–10 mm. Motile organisms are not caught as effectively as nonmotile forms. *Velella* may be an important predator on fish eggs, which make up a major part of its diet. Euphausiid eggs are also an important part of its food. Off the California coast the seasonal appearance of *Velella* on the surface is correlated with the spring spawning of pelagic fish, such as hake, saury, sardine, and jack mackerel. The relatively greater abundance of suitable food during the spring months may be one of the factors responsible for the seasonal cycle of reproduction and growth in *Velella*.

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Interspecific Differences in the Reaction to Atropine and in the Histology of the Esophagi of the Common California Sea Hares of the Genus *Aplysia*

LINDSAY R. WINKLER and BERNARD E. TILTON[1]

DURING A STUDY of the effects of certain cholinergic agents on the tissues of *Aplysia*, it was noted that the esophagi of the two California species (*A. californica* and *A. vaccaria*) reacted divergently to atropine. This is of interest to both the taxonomy and physiology of the genus as well as potentially to a better understanding of the mode of action of atropine. Other drugs commonly known to show activity on muscle tissue were also tested on the two species to determine if any other interspecifically divergent reactions existed. These pharmacological reactions will be reported later.

Botazzi (1898) observed the periodic contractions of the esophagus of the European *Aplysia* and made a thorough study of its physiology. The physiology of the crop was studied extensively by von Brücke (1905). Straub (1907) reported the reaction of the heart of an unspecified species of *Aplysia* to muscarine and noted the lack of atropine antagonism in the heart ventricle. Hogben (1924) studied the reaction of the crop of an European *Aplysia* to epinephrine.

MATERIALS AND METHODS

Small- to medium-size specimens of *Aplysia (Neaplysia) californica* Cooper and *Aplysia (Aplysia) vaccaria* Winkler were collected during the summer months at Lunada Bay, Palos Verdes, Los Angeles Co., California. The animals were packed in wet *Pelvetia fastigata* and transported to the laboratory where they were maintained in a 10-gal. salt water aquarium until needed. A Cole-Parmer model all-plastic impeller-type pump drew the water from the aquarium through a filter containing glass wool and activated charcoal and pumped it serially through two 5 gal. carboys maintained in a refrigerator. It was thus possible to keep the water clean and cooled to approximately the temperature of the intertidal environment of these animals. Parsley obtained in the local market was eaten in quantity by *A. californica* but was refused by *A. vaccaria*. Consequently all specimens of the latter were used as soon as practicable.

Animals were sacrificed by incising the entire length of the foot, turning the animal inside out and removing the esophagus after tying it at both ends. The esophagi were suspended from a plastic holder in conventional baths using 30 ml. of sea water. The movable end of the esophagus was ligated to a Grass force-displacement transducer, which was connected to a Grass amplifier-recorder.

To identify the two types of excursions noted in the tracings, cross sections of esophagus tissue were tied on opposite sides of the ring thus formed so as to obtain tracings of the contractions of the circular muscle with little or no effect from the longitudinally oriented tissue. Atropine was used in 1:1000 solution (1 mg/ml) in all cases.

For histological examination both longitudinal and cross sections were made using standard techniques. These were stained with eosin and hematoxylin. Sections were also made of all the noticeably differentiated areas of the digestive tract.

EXPERIMENTAL RESULTS

The normal pattern of contraction as recorded from the isolated esophagus consists primarily of comparatively rapid short excursions which vary in frequency and amplitude. These may be interspersed with occasional contractions of greater amplitude, especially in *A. californica* (Fig. 1*a*). Since the latter contractions were ab-

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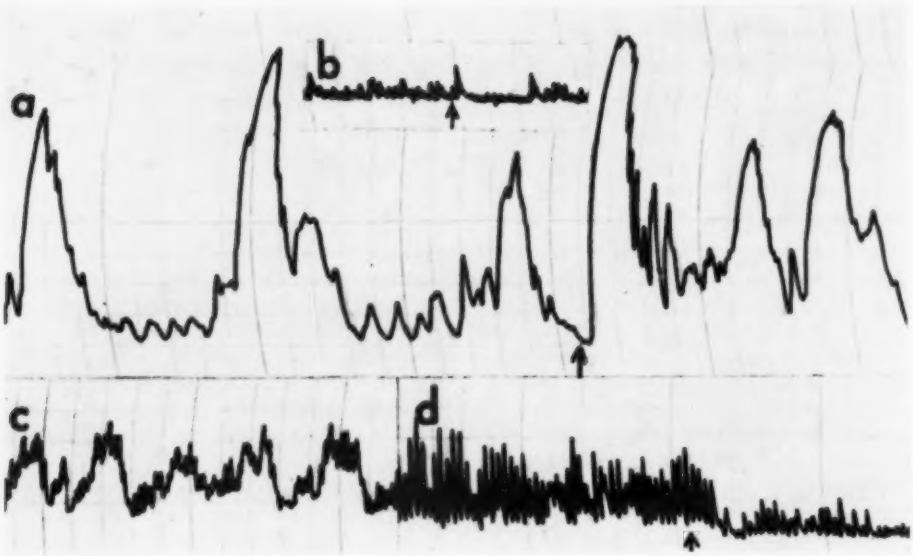

FIG. 1. The normal tracing of the esophagus of *A. californica* is indicated in *a* and the effect produced by 0.2 mg. of atropine solution added to the 30 ml. bath is shown at the arrow. The depressing of the circular contractions of a ring of esophagus by 0.2 mg. atropine is shown in *b*. Tracings *c* and *d* show two types of normal tracings obtained from *A. vaccaria* esophagus and the effect of 0.4 mg. atropine added at arrow.

sent when the rings of esophagus were used (Fig. 1*b*), they are attributed to longitudinally oriented muscle in contrast to a primary circular muscle response. For some unknown reason the rapidity of contraction was increased when the esophagus was arranged in rings. The deep, intermittent excursions are not as pronounced in *A. vaccaria* (Fig. 1*c*) and may be absent (Fig. 1*d*). The response of circular muscle, however, is consistently more rapid and more pronounced than is the case in *A. californica*.

In *A. californica* even very small doses (0.05 mg. in some cases) of atropine produce an immediate and unfailing but transitory contraction of the longitudinal muscle (Fig. 1*a*). The esophagus of *Aplysia vaccaria*, however, does not react to atropine except in comparatively large doses of 0.4 ml. or more (in a 30 ml. bath), in which case the excursions of the circular muscle are depressed (Fig. 1*d*). The circular muscle of *A. californica*, as demonstrated by the muscular ring preparations, is noticeably depressed by atropine in even smaller doses than that required to depress the circular type muscle in *A. vaccaria* (Fig. 1*b*). This depression was not noticed in the usual tracings of *A. californica* muscle since it was obscured by the longitudinal contractions. Other muscle-active drugs with specific reactions of interest in themselves (which are to be reported later) did not produce divergent results between the two species.

In an attempt to gain an insight into possible reasons for the divergence of reaction between the two species, histological sections were made and stained with eosin and hematoxylin. Strongly eosinophilic bundles of coarse, cylindrical muscle strands were observed in the esophagus of *A. californica* (Fig. 2*a, b*). These strands appear coarsely striated in some preparations (Fig. 2*b*) and coarsely granular in others, the differences possibly representing problems in killing and fixing. The nuclei are larger and more sparse than those of *A. vaccaria* (Fig. 2*c, d*) and of the surrounding more conventional muscle of the present species. Not only are the nuclei three times as large but they tend to be arranged across the muscle strands, thus appearing rectangular in section. This muscle is

contrasted with the less eosinophilic, more undulatory muscle of the circular (Fig. 2*a*) and *A. vaccaria* type muscle (Fig. 2*c, d*), which is very heavily nucleated. While strands of a type of muscle which seems morphologically to be somewhat similar to the former type of muscle appear sparsely in the crop, and to even a lesser extent in the area between the gizzard and "stomach" of the digestive tract in *A. californica*, none of the eosinophilic muscles observed in other parts of the digestive tract of *A. vaccaria* possessed the distinctive tubular shape with the vacuolation, striation or granulation, and lack of undulatory characteristics.

DISCUSSION AND CONCLUSIONS

While it might be tempting to assume that the histological differences represent the immediate cause of the divergent pharmacological reactions observed, they are better interpreted as visible, easily demonstrable, morphological differences which parallel and are closely associated with neurohumoral and even biochemical differences which are themselves the underlying mechanistic causes. This is especially true since the effect of atropine on conventional tissue systems is thought to be on the neuromuscular receptors. The contractatory response observed in *A. californica* appears to be the transitory result of stimulation, since the mechanical stimulation of washing will produce similar contractions. However, the sensitivity to this chemical stimulation is very great, being as low as 0.05 mg. atropine placed in the 30 ml. bath—a concentration of $1{:}6\times10^{5}$. Such a sensitivity represents a very delicately balanced chemical system.

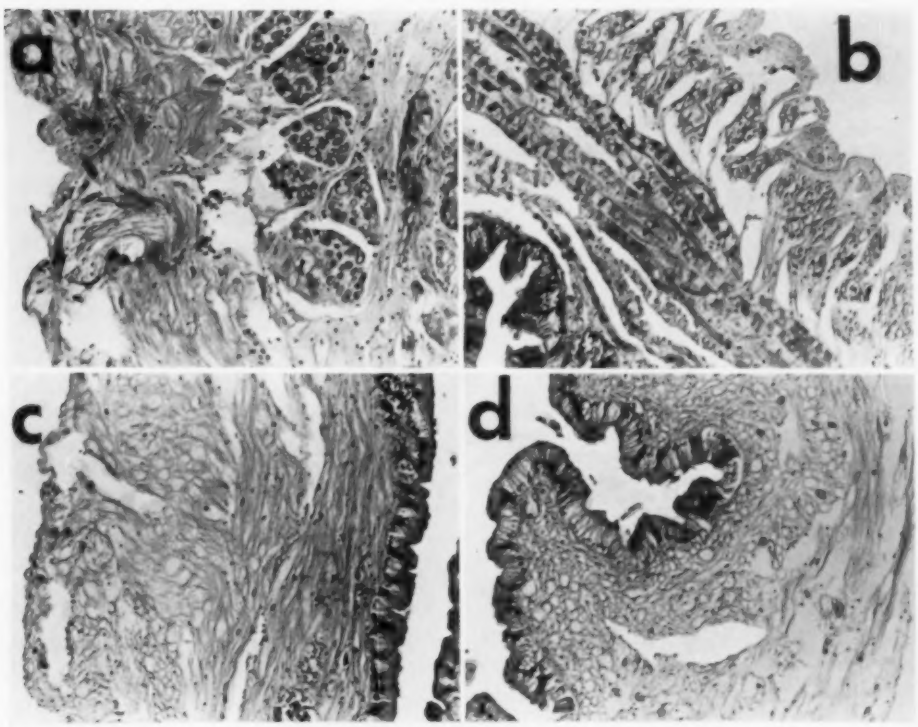

FIG. 2. *A. californica: a*, cross section; *b*, longitudinal section. *A. vaccaria: c*, longitudinal section; *d*, cross section. The midsection of the esophagi were used for cross sections.

Moreover, the mechanism is of special interest since it is unique among known muscle preparations in that it is stimulated rather than depressed by atropine.

The drug reaction and histological difference accentuates the divergence present within the genus. *A. vaccaria* belongs to a large and widespread subgenus (*Aplysia*), while *A. californica* (subgenus *Neaplysia*) is unique to the Californias. When it becomes possible to study comparatively the members of the two other subgenera[2] (*Varria* and *Pruvataplysia*), a taxonomic generalization may be possible. However, Bottazzi (1898) in his physiological study of the esophagus indicated that *A. limacina* (almost certainly *A. fasciata* of subgenus *Varria*) was much more atonic than the close relative of *A. vaccaria* (subgenus *Aplysia*) with which he also worked. Since it is thought that *A. californica* is an offshoot of this subgenus *Varria*, and since its esophagus is far from atonic by any interpretation, it may be that the musculature of the former has diverged considerably from its forerunners.

It would also seem quite probable that more comparative studies of the tissues of the species contained in other genera of animals would reveal occasional divergences of at least equal magnitude. Such a possibility cannot safely be overlooked in experimental biology in any of its phases, and accentuates the need for accurate taxonomy before proceeding with studies which may be of a nontaxonomic nature.

[2] Specimens of esophagus tissue from these subgenera were kindly supplied from existing museum material on hand by Dr. N. B. Eales but, unfortunately, the conventional preservation method employed by the collectors was not adequate for any type of conclusions.

SUMMARY

1. The normal pattern of esophageal contractions in *Aplysia californica* consists of short rapid contractions attributed to circular muscle, interspersed at intervals by deep excursions attributed to the longitudinal musculature. These secondary contractions are less pronounced and less regular in *A. vaccaria*.

2. Atropine causes marked contraction of the esophagus in *A. californica*, even in low concentration, but in *A. vaccaria* it depresses circular activity in higher concentrations.

3. The esophagus of *A. californica* has longitudinal bundles of cylindrical muscle appearing coarsely striated or granular. These have not been found in *A. vaccaria*, and are suggested as being associated with the mechanistic cause for the differences in reaction noted.

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The Vegetation of Yanagi Islet, Truk, Caroline Islands

PETER J. R. HILL[1] and BENJAMIN C. STONE[2]

YANAGI ISLET, located midway between Moen and Dublon in Truk lagoon (7° 24′ N.; 151° 53′ E.) is a small islet roughly 30 ft. high, about 800 ft. long and 300 ft. wide, with scarcely any strand but with volcanic rock pavement on all shores, and on the south side, numerous loose volcanic boulders. Much of the volcanic rock of which the islet is formed appears to be a breccia resembling conglomerate. The reef surrounding the islet is rather large, with small storm-deposited rocks on the northeast sides. There is a smallboat pass on the west side and another pass, probably safe for small craft, on the north side. During World War II, the Japanese tunnelled through the islet from a cave on the south side to the north side; another Japanese cave on the south side does not run all the way through the islet. A small-gauge railroad ran from the tunnel into the lagoon, for loading operations. The track is now rusty and twisted.

The vegetation, despite the obvious prior use of the islet for military purposes, is relatively undisturbed in a few small areas. The Trukese do not live on the islet, but visit it occasionally for fish and shell-fish, and perhaps for mangoes. There are only a few coconut palms and a few of their seedlings.

The vegetational zonation of the islet appears to comprise three areas: (1) a fringe area, more or less encircling the islet at sea level. (2) An open, rock-strewn extremity on the east, with a herbaceous cover, which slopes toward the east and terminates abruptly as a low cliff. This area is similar to the Tunnuk-Penniasene and Mechitiu lava flows, but here there is no polygonal-patterned basalt. (3) An inner upland, with a developed tree-cover and fairly good soil. There is in fact a transitional area of low-crowned shrubs between zones 2 and 3; it is not known whether this is a natural attenuation in plant size, accompanied by increasing dominance of the herbaceous cover, which has persisted, or whether it is a result of human disturbance. However, the area contains a U. S. Navy Survey bench-mark on a concrete base (without further information).

The most interesting features of the islet are the complete absence of coralline rock and soil, and the absence of most of the halophytic species of littoral plants which are so common elsewhere in Truk, a lack which is no doubt correlated with the nature of the substrate. The plants of Yanagi are by no means unique, and may be commonly found in Truk, and indeed through much of Micronesia. They are not restricted to volcanic soils, for some of them, at least, are known from the atolls nearby as well. But the strand species such as *Scaevola Taccada*, *Messerschmidia argentea*, *Terminalia samoensis*, and *Soulamea amara* are notably absent. Most of the species which occur on Yanagi also occur on the reef islets of Truk in coralline soil; but the lack of these littoral plants, which might reasonably be expected to grow there, is the curious and interesting feature of Yanagi Islet.

VEGETATION ZONES: Since the islet is so small, altitudinal considerations are of no account above sea level. The fringe area (1) seems to differ from the inner upland area (3) chiefly because of the exposure of the former and its hindrances to undisturbed plant growth, partly because of subjection to change from wind and waves, and to the concomitant salt spray, and partly because of the abundant volcanic boulders but thin, scanty soil. The grassland (2) and the intermediate area of shrubs may be the result of disturbance, or, again, may be the result of hard, thin soil with numerous embedded rocks, combined with exposure to wind and illumination. Salt spray is apparently minimized by the

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reef, which lies many feet from the islet's shore. No rainfall records are available; however, the inner forest with its better development of soil- and tree-cover no doubt accumulates moisture and retains it longer than the grassland and fringe area, with their porous volcanic boulders.

1, Fringe Area. A, Upper story: **Desmodium umbellatum* (L.) DC., common, the trunk to 10 cm. diameter; **Colubrina asiatica* (L.) Brongn., common, shrubby; **Clerodendron inerme* (L.) Gaertn., common scandent shrub; **Callicarpa candicans* (Burm.) Hochr., scattered; **Barringtonia asiatica* (L.) Kurz, scarce, only small plants seen; **Guettarda speciosa* L., only on south side; **Allophylus timorensis* (DC.) Bl., on south side; **Ficus* sp., on south side; **Premna obtusifolia* R. Br., on south side only; **Wedelia biflora* (L.) DC. ex Wight, scandent shrub; **Morinda citrifolia* L.—B, Vines: *Abrus precatorius* L.; **Ipomoea digitata* L.; **Passiflora foetida* L.; *Dioscorea* sp.; **Ipomoea pes-caprae* L., only one plant seen, in a small area; **Derris elliptica* (Roxb.) Bentham.—C, Ground cover: **Microsorum scolopendria* (Burm.) Copel.; *Vernonia cinerea* (L.) Less.; *Echinochloa colonum* (L.) Link; **Tacca leontopetaloides* (L.) Ktze., scattered and rare; **Digitaria pruriens* (Trin.) Büse. —D. Epiphytes: **Asplenium* sp.; **Davallia solida* (Forst.) Sw.; **Dendrobium* sp.

2, Grassland. A, Herbaceous cover, extreme eastern end of islet: **Digitaria pruriens* (Trin.) Büse; *Paspalum dilatatum* (?); *Chrysopogon aciculatus* (Retz.) Trin.; *Paspalum conjugatum* Berg.; *Cyperus* sp.; **Fimbristylis atollensis* St. John; *Emilia sonchifolia* DC.; *Phyllanthus amarus* Schum. & Thonn.; **Portulaca samoensis* v. Poelln.; **Microsorum scolopendria* (Burm.) Copel., a dwarf form.—B, Transitional zone, with shrubs; merging with 3: *Desmodium* sp. (seedlings); *Hedychium coronarium* Koen. & Retz.; **Barringtonia asiatica* (L.) Kurz, one seedling; **Tacca leontopetaloides* (L.) Ktze.; *Abrus precatorius* L.; **Premna obtusifolia* R. Br.; **Passiflora foetida* L.; *Abelmoschus* sp.; *Capsicum frutescens* L.; *Cocos nucifera* L.(a few young trees); **Morinda citrifolia* L.; **Colubrina asiatica* (L.) Brongn.; **Canavalia microcarpa* (DC.) Piper.

* Species marked with an asterisk are indigenous.

3, Inner Upland Forest Area.—A, Trees: *Mangifera indica* L.; *Musa balbisiana* X *acuminata; Carica Papaya* L.; **? Terminalia catappa* L.; **Ficus tinctoria* Forst.; *Erythrina variegata* L.; *Cocos nucifera* L.—B, Shrubs: **Colubrina asiatica* (L.) Brongn.; **Morinda citrifolia* L.; **Glochidion ramiflorum* Forst.; **Polyscias grandifolia* Volkens.—C, Ground cover: **Oplismenus compositus* (L.) Beauv.; *Paspalum conjugatum* Berg.; *P. dilatatum* (?).—D, Vines: **Canavalia microcarpa* (DC.) Piper; *Abrus precatorius* L.; **Piper fragile* Benth.—E, Epiphytes: **Davallia solida* (Forst.) Sw.; **Microsorum scolopendria* (Burm.) Copel.

All plants mentioned are represented by specimens in possession of the senior author.

ANIMALS PRESENT: The terrestrial animals, excluding insects and other invertebrates, were noted and identified by William R. Newman. Two species of lizard were fairly common, *Emoya cyanura* and *E. boetgeri*. The birds noted were *Aplonis opacus angus*, the Micronesian starling; *Demigretta sacra sacra*, the reef heron (dark phase); *Myzomela cardinalis major*, the cardinal honey-eater; *Collocalis inquieta rukensis*, the Carolines swiftlet; and *Gygis alba*, the fairy tern.

SUMMARY

The small volcanic islet in Truk Lagoon called Yanagi is remarkable for the lack of coralline development and the lack of halophytic vegetation which are common elsewhere on Truk. The vegetation appears to comprise three zones, which are called the fringe area, the grassland area, and the upper inland forest. The summit is about 30 ft. above sea level, and the islet is surrounded by a reef. Though occupied during the war, the vegetation is now fairly recovered from disturbance. A list of the plants occurring in each vegetation zone, and a brief note on some animals observed, is given.

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Revision of the Genus *Pandanus* Stickman, Part 6
New *Pandanus* Species from Queensland, Australia

HAROLD ST. JOHN[1]

THIS PART of the author's revision of the genus *Pandanus* is a collection of new species, all from the tropical northeastern corner of Queensland. They were all collected by L. J. Brass.

Pandanus sphaericus sp. nov. (sect. *Australibrassia*)

Figs. 23–24

NOM. VERN.: "maia."

DIAGNOSIS HOLOTYPI: Arbor 6–7 m. alta, trunco gracile "eo et ramis cum spinis brevibus conicis, ramis reflexis, radicibus fulturosis paucis 2–3 cm. longis," foliis 1.5 m. longis 3 cm. latis subcoriaceis gladiatis in apice subulato longiter attenuatis, puncto 10 cm. ex apice 1.5 mm. lato, basi inermi, sed ex 5 cm. marginibus cum subulato-serris pallidis 0.5–1 mm. longis 2–4 mm. distantibus, midnervio inermi, in regio mediali marginibus cum serris 0.5–0.7 mm. longis 1.5–3 mm. distantibus apicibus subulatis, midnervio infra cum serris 0.2–0.3 mm. longis 2–7 mm. distantibus adscendentibus, proxima apice marginibus et midnervio infra cum serris 0.2–0.3 mm. longis 2–3 mm. distantibus adscendentibus apicibus subulatis, pedunculo 26 cm. longo curvato cum bracteis foliosis paucis, syncarpio 12 cm. diametro subgloboso pendente circa 15 phalangibus ferentibus, eis 4.3–4.6 cm. longis 3.9–4.3 cm. latis 3.1–3.2 cm. crassis suborbicularibus sed subcompressis 4–5-angulosis in sicco pallide brunneis exlucidis laevibus, lateribus valde curvatis parte ⅔ supera libera, apice truncato, suturis lateralibus nullis, sinibus centralibus apicalibus 4–5 mm. profundis anguste V-formatis, carpelis 9–11, apicibus anguste pyramidalibus sed cum regione proximali truncato et dimidio proximali duro brunneo lucido ad stigmatam dirigito, stigmatibus 1.5 mm. longis ellipticis ad ovatis sulcatis in apice latere proximo, suturis proximis ½–¾ ad fondam extentis, endocarpio submediali 2.5–3 cm. longo osseoso pallide muris lateralibus 4–5 mm. crassis, seminibus 13–17 mm. longis 4 mm. diametro ellipsoidis, mesocarpio supero caverna unica 1 cm. longa cum fibris multis traversis formanto, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 6–7 m. tall; trunk slender, it "and the branches studded with short conical thorns; branches down-turned; prop roots few, 2–3 dm. long"; leaves 1.5 m. long, 3 cm. wide, subcoriaceous, rapier-like and tapering from the base to the long subulate tip which 10 cm. down is only 1.5 mm. wide, the base unarmed, but beginning 5 cm. from the base the margins with subulate serrations, pale, 0.5–1 mm. long, 2–4 mm. apart; the nearby midrib unarmed; at the midsection the margins with subulate-tipped serrations 0.5–0.7 mm. long, 1.5–3 mm. apart; the midrib below with ascending serrations 0.2–0.3 mm. long, 2–7 mm. apart; near the tip the margins and midrib below with subulate-tipped ascending serrations 0.2–0.3 mm. long, 2–3 mm. apart; peduncle 26 cm. long, curving, with a few leafy bracts; syncarp pendent, 12 cm. in diameter, subglobose, of about 15 phalanges, these 4.3–4.6 cm. long, 3.9–4.3 cm. wide, 3.1–3.2 cm. thick, suborbicular, but somewhat compressed, 4–5-angled, when dried light brown, dull, smooth, the 4–5 sides strongly curving, upper ⅔ free; the apex truncate, lateral sutures none; central apical sinuses 4–5 mm. deep, narrow V-shaped; carpels 9–11, the apices narrow pyramidal with a proximal truncation and its inner half leading to the stigma hard, brown, shining; stigmas 1.5 mm. long, elliptic to ovate, creased, at tip of steep proximal face of apex; below it the proximal suture running ½–¾ way to valley bottom; endocarp submedian, 2.5–3 cm. long, bony, pale throughout, the lateral margins 4–5 mm. thick; seeds 13–17 mm. long, 4 mm. in diameter, ellipsoid; upper mesocarp a single cavity 1 cm. long, with many strong longitudinal fibers; basal mesocarp fibrous and fleshy.

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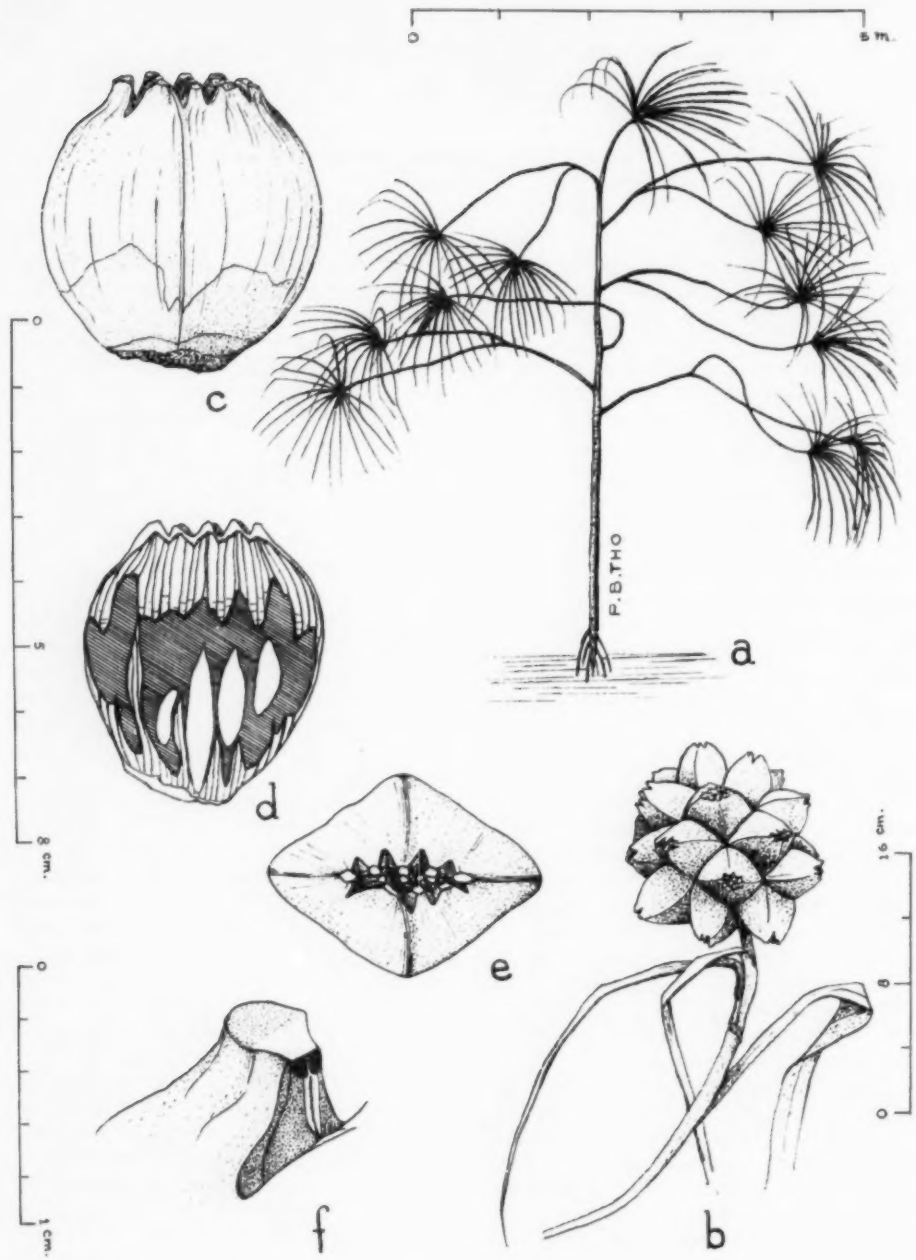

FIG. 23. *Pandanus sphaericus*, from holotype. *a*. Habit, × 1/70; *b*, syncarp, × ¼; *c*, phalange, lateral view, × 1; *d*, phalange, longitudinal median section, × 1; *e*, phalange, apical view, × 1; *f*, carpel apex and stigma, oblique view, × 4.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, abundant locally in rain forest behind the coastal sand dunes, 20 m. alt., May 9, 1948, *L. J. Brass 18,715* (BRI).

DISCUSSION: *P. sphaericus* is a member of the section *Australibrassia* and there also is its nearest relative, *P. cochleatus* St. John, which is distinguished by having the phalanges pyriform; the carpels 12–16; stigma below an overhanging cochleate rim; prop roots absent; and leaves having near the base marginal teeth 1.3–2 mm. long. It also occurs on the Cape York Peninsula. *P. sphaericus* differs by having the phalanges suborbicular; carpel 9–11; stigma on proximal face of carpel apex without an overhang; prop roots few; and leaves near base with marginal teeth 0.5–1 mm. long.

The new epithet is the Latin adjective, *sphaericus*, spherical, in reference to the shape of the phalange and of the syncarp.

Pandanus ferrimontanus sp. nov. (sect. *Pandanus*)
Figs. 25–26

DIAGNOSIS HOLOTYPI: Arbor 5–7 m. alta 10–12 cm. diametro in corona laxa ramosa, radicibus fulturosis nullis, foliis 133–160 cm. longis 5.8 cm. latis subcoriaceis glaucis supra infraque gladiformatis gradatim ex basi in apice subulato longe acuminato diminuentibus, in puncto 10 cm. ex apice 3 mm. latis, marginibus ex basi per 29 cm. inermibus tum cum aculeis 2–3 mm. longis 6–21 mm. distantibus subulatis adscendentibus apice brunneo, midnervio inermi, in sectio mediali margine unica cum aculeis 1–2 mm. longis 2–6 mm. distantibus adpresse adscendentibus subulatis cum basi crassa, margine altera cum aculeis paucis simulantibus sed minoribus vel in partibus inermibus, midnervio infra cum aculeis paucis remotis minutis adscendentibus, in regione apicali marginibus et midnervio infra cum aculeis 0.2–0.3 mm. longis 3–5 mm. distantibus subulatis validis adscendentibus, pedunculo 40 cm. longo excedenti obscure trigono folioso, syncarpio 16 cm. longo 14 cm. diametro terminali solitario ovoideo-globoso cum circa 45 phalangibus, eis 4.5–4.7 cm. longis 4.2 cm. latis 3.4–3.5 cm. crassis late obovoideis subcompressis, apice rotundato, parte ⅓ supera libera, lateribus cum 5–6 angulis majoribus et carpela quoque cum 2–4 angulis et valleculis angustis et tum lateribus phalangiorum proximorum interobseratis, in sicco lateribus papillosis et parte supera rubro-brunnea, suturis lateralibus angustis in dimidia supera, sinibus apicalibus centralibus 3.5–4.5 mm. profundis fondis angustis sinuosis et lateribus interobseratis, carpelis 8–12 plerumque 9–10, apicibus subaequalibus semiorbicularibus pallide brunneis sed lateribus brunneo-rimosis, regione obliqua brunnea concava ex stigmate distalia, stigmatibus 1–1.5 mm. longis ellipticis vel truncatis obscure brun-

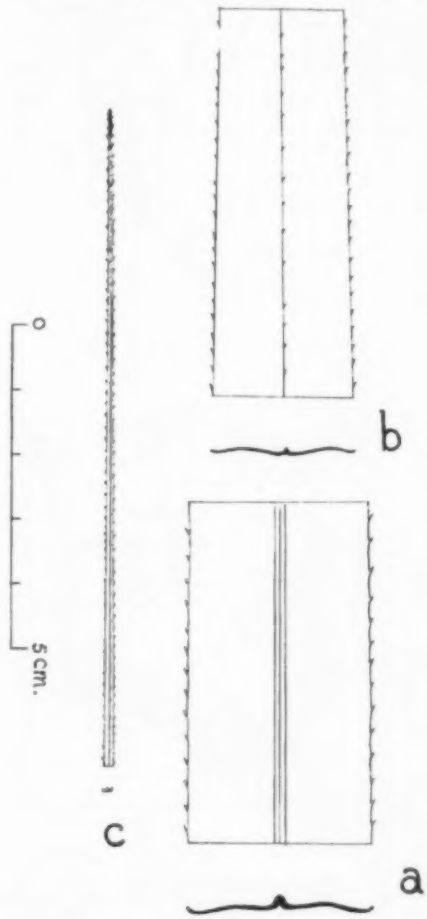

FIG. 24. *Pandanus sphaericus*, from holotype, lower side of leaf, × 1. *a*. Near base; *b*, middle; *c*, apex.

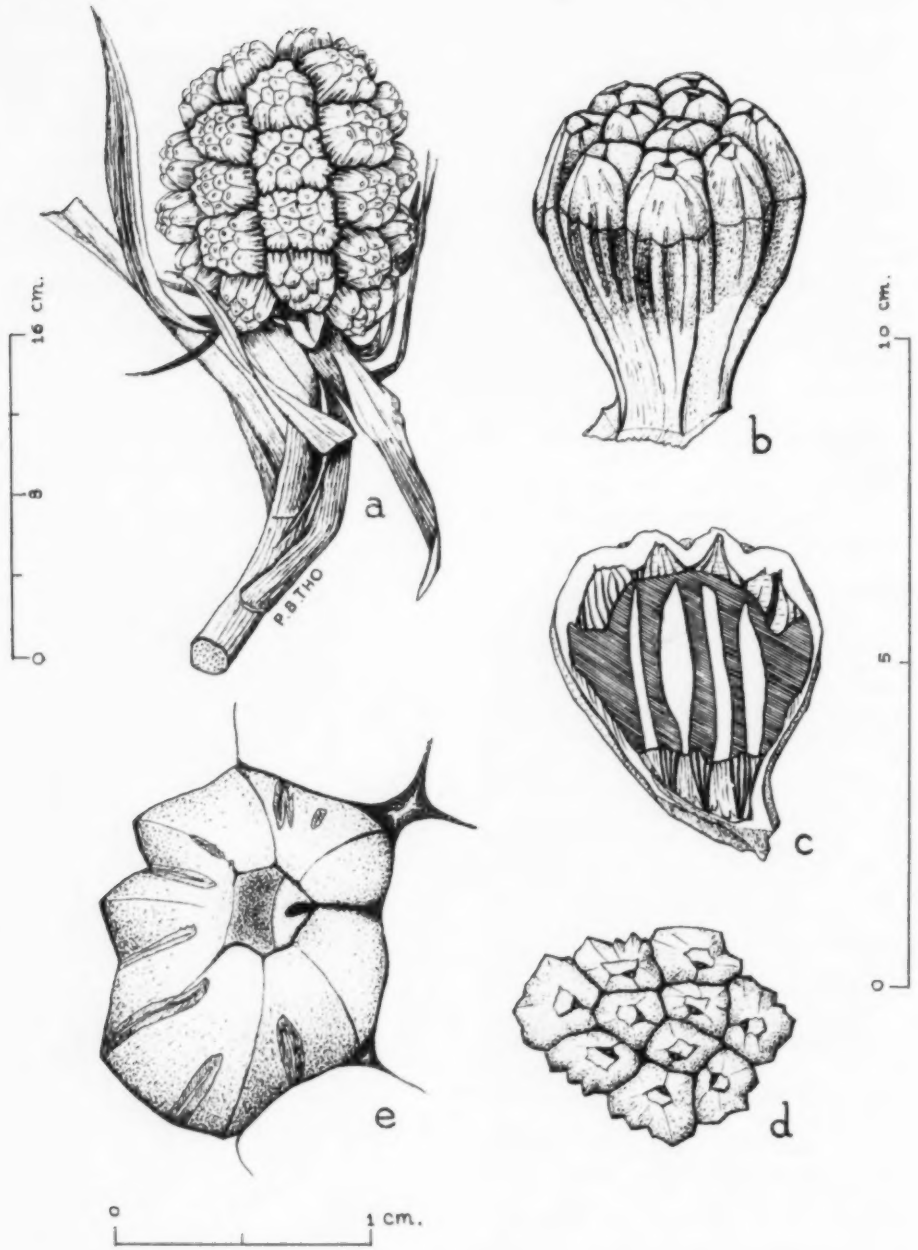

FIG. 25. *Pandanus ferrimontanus*, from holotype. *a*, Syncarp, × ¼; *b*, phalange, lateral view, × 1; *c*, phalange, longitudinal median section, × 1; *d*, phalange, apical view, × 1; *e*, carpel apex with stigma, apical view, × 4.

neis obliquis sulcatis centripetalibus, sinu proximo profundo ½ vel omnino distancia ad fondam extento, endocarpio 22–25 mm. longo supramediali osseoso stramineo lateribus lateralibus 8–10 mm. crassis, interiore cavernarum seminarum brunneo, seminibus 18–20 mm. longis 3–5 mm. diametro irregulariter ellipsoideis, mesocarpio apicali in carpella quoque cavernam cum fibris paucis et membranis stramineis transversis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 5–7 m. tall, 10–12 cm. in diameter, branched into an open crown; prop roots none; leaves 133–160 cm. long, 5.8 cm. wide, subcoriaceous, glaucous above and below, sword-like, gradually tapering from near the base to the long acuminate, subulate tip which 10 cm. down is 3 mm. wide, the basal margins unarmed for 29 cm., then with prickles 2–3 mm. long, 6–21 mm. apart, subulate, ascending, brown-tipped; the nearby midrib unarmed; at the midsection one margin is with prickles 1–2 mm. long, 2–6 mm. apart, broad based subulate, appressed ascending, the other margin with a few similar but smaller prickles or intermittently with none; the midrib below with a few remote, minute, ascending prickles; near the apex the margins and midrib below with prickles 0.2–0.3 mm. long, 3–5 mm. apart, stout subulate, ascending; peduncle more than 40 cm. long, obscurely trigonous, leafy bracted; syncarp solitary, terminal, 16 cm. long, 14 cm. in diameter, ovoid-globose, the color unknown, of about 45 phalanges, these 4.5–4.7 cm. long, 4.2 cm. wide, 3.4–3.5 cm. thick, broadly obovoid, somewhat flattened, the apex rounded, upper ⅓ free, the sides with 5–6 major angles and each carpel with 2–4 sharp secondary ridges and valleys so that adjacent phalanges fit as if mortised, when dry the sides papillose and the upper part reddish brown; lateral sutures narrow but extending half way down; central apical sinuses 3.5-4.5 mm. deep, the bottoms narrow and sinuous mortised; carpels 8–12, mostly 9–10, the apices subequal, semiorbicular, the sides with dark brown cracks, elsewhere pale brownish, with an oblique distal, brown concavity leading to the stigma; stigma 1–1.5 mm. long, elliptic or truncate elliptic, creased, dark brown, oblique, centripetal; proximal sinus deep, running ½ way

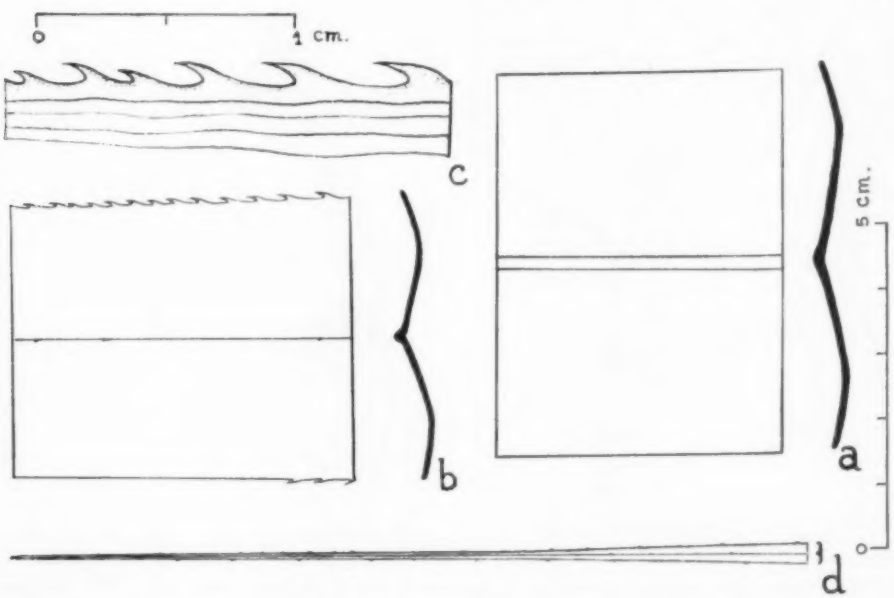

FIG. 26. *Pandanus ferrimontanus*, from holotype, lower side of leaf. *a*. Near base, × 1; *b*. middle, × 1; *d*. apex, × 1; *c*, marginal serrations at middle, × 4.

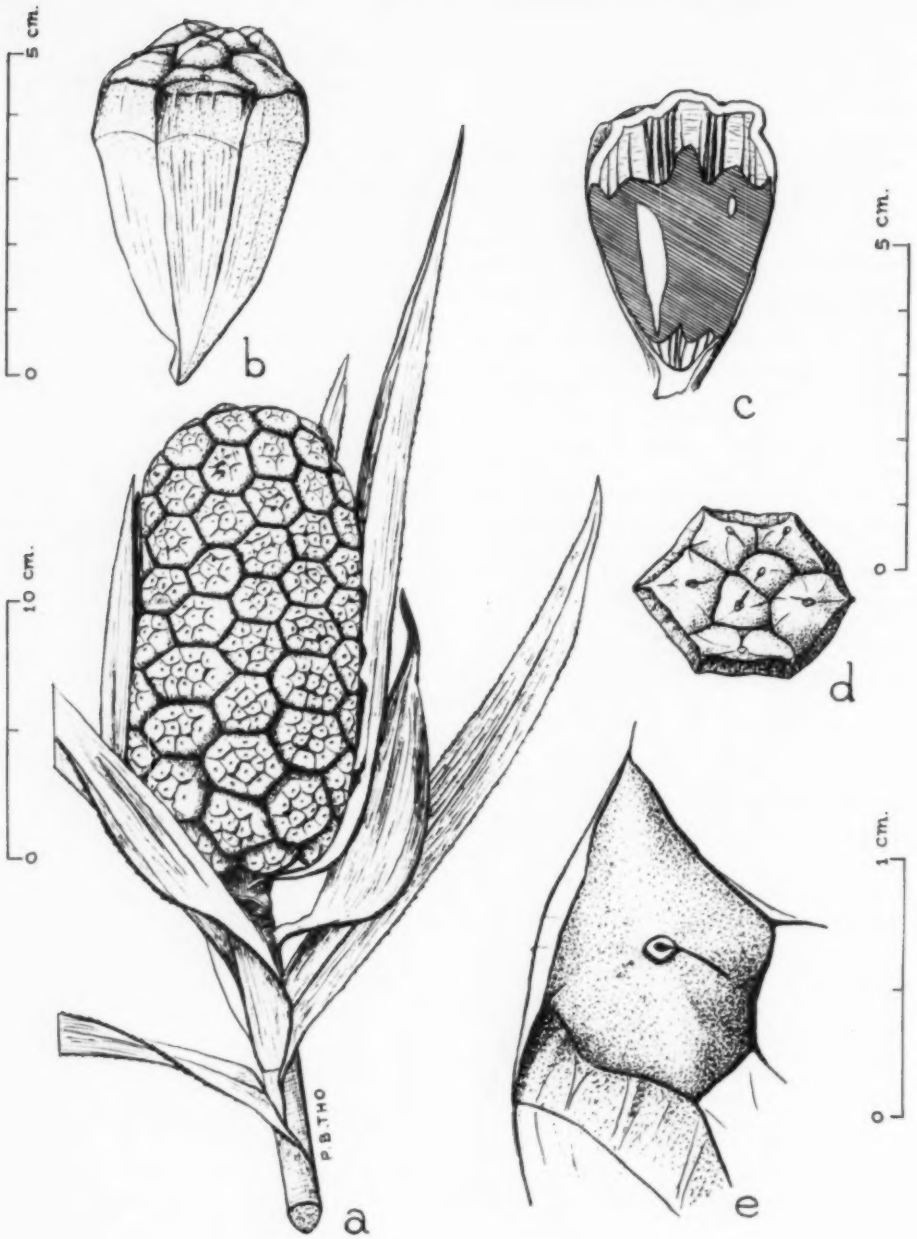

FIG. 27. *Pandanus oblatus*, from holotype. *a*, Syncarp, × 2/5; *b*, phalange, lateral view, × 1; *c*, phalange, longitudinal median section, × 1; *d*, phalange, apical view, × 1; *e*, apex of carpel and stigma, apical view, × 4.

to all the way to the valley bottom; endocarp supramedian 22–25 mm. long, bony, stramineous except for the dark brown, shining lining of the seed cavities, lateral walls 8–10 mm. thick; seeds 18–20 mm. long, 3–5 mm. in diameter, irregularly ellipsoid; apical mesocarp in each carpel forming a cavern with a few strong, longitudinal fibers, and transverse, stramineous, medullary membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Iron Range, scattered or gregarious in groves in savanna forest, 20 m. alt., June 24, 1948, *L. J. Brass 19,312* (BRI).

DISCUSSION: The flowers were not seen by the collector. This new species is a member of the section *Pandanus*, to which most of the Australian species belong. None of the previously described species are close relatives, so no contrast is needed here.

The new specific epithet is formed from the Latin, *ferrum*, iron; *montanus*, of the mountain, in reference to the name of the type locality.

Pandanus oblatus sp. nov. (sect. *Pandanus*)
Figs. 27–28

DIAGNOSIS HOLOTYPI: Arbor 12–14 m. alta, trunco "crasso, corona ramosa, radicibus fulturosis multis longis spinosis," foliis 1.6 m. longis 9.2 cm. latis crassiter coriaceis infra subglaucis, in section valde M-formatis, gladiformatis gradatim in apice subulato trigono valide diminuentibus, in regione 10 cm. ex apice 5–6 mm. latis, basi amplexicauli et integri sed ex 7 cm. marginibus cum aculeis 2–3 mm. longis 3–6 mm. distantibus subulatis validis luteis subadscendentibus, midnervio infra inermi, in regione mediali marginibus cum aculeis 1.5–3 mm. longis 3–5 mm. distantibus subulatis validis arcuato-adscendentibus, midnervio infra salienti acuito et cum aculeis 2.5–3 mm. longis 10–20 mm. distantibus simulantibus adscendentibus; in regione apicali marginibus et midnervio infra subulato-serratis serris 0.8–1.2 mm. longis 2–3 mm. distantibus, pedunculis 15 vel plus cm. longis obtuse trigonatis folioso-bracteatis, syncarpio 18 cm. longo 13 cm. diametro cylindrico sed apicibus ambis rotundatis cum circa 92 phalangibus, eis 4.7–5.1 cm. longis 2.9–3.5 cm. latis 2.4–2.7 cm. crassis obovoideis in sicco rubro-

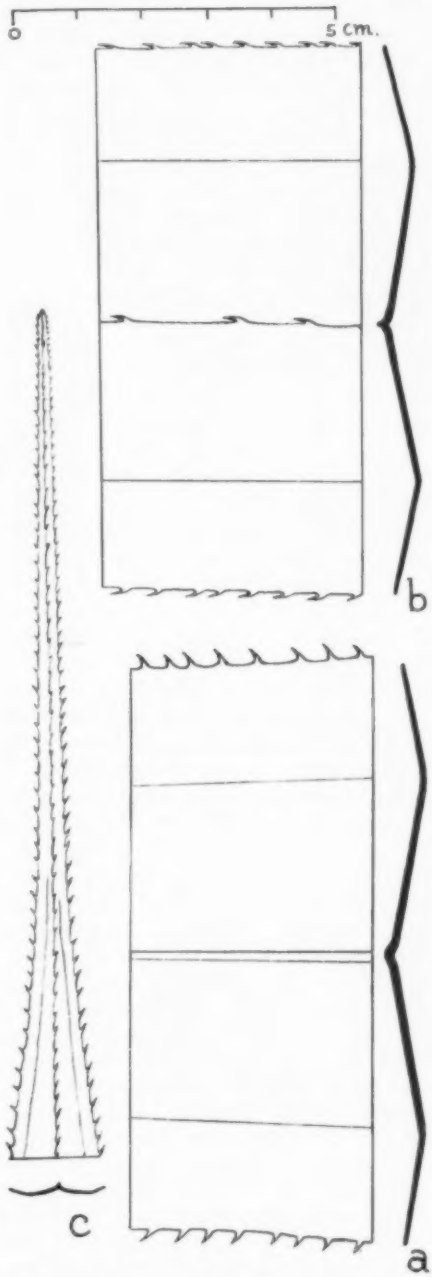

FIG. 28. *Pandanus oblatus*, from holotype, lower side of leaf, × 1. *a*, Near base; *b*, middle; *c*, apex.

brunneis 4–6-angulosis, lateribus papillosis subcurvatis vel paene planatis parte ¼ supera libera, apice rotundato, suturis lateralibus nullis, sinibus apicalibus centralibus 2–4 mm. profundis late V-formatis, carpelis 5–12 sed in phalangibus dimidiae superae plerumque 6–7 et in eis inferis plerumque 10–11, apicibus centralibus oblato-semiorbicularibus, eis marginalibus oblato-pyramidalibus, stigmatibus 1–1.8 mm. longis suborbicularibus ad ovalibus sulcatis obscuris apicalibus centripetalibus plerumque obliquis, sinu proximali lato ½ distancia ad fondam extento, endocarpio mediali osseoso obscure brunneo excepta marginibus pallidis, lateribus lateralibus 4–5 mm. crassis, seminibus 16 mm. longis 4 mm. diametro ellipsoideis, mesocarpio apicali in carpela quoque caverna cum membranis pallidis medullosis formanti, mesocarpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 12–14 m. tall; trunk "thick, crown branched; stilt roots many, long, and prickly"; leaves 1.6 m. long, 9.2 cm. wide, thick coriaceous, below slightly glaucous, in section sharply M-shaped, sword shaped, gradually narrowed to the stout, trigonous, subulate apex, this 10 cm. down is 5–6 mm. wide, at very base amplexicaul and entire, but from 7 cm. up the margins with prickles 2–3 mm. long, 3–6 mm. apart, stout subulate, yellow, slightly ascending, the nearby midrib unarmed below; at midsection the margins with prickles 1.5–3 mm. long, 3–5 mm. apart, stout subulate, arcuate ascending; the midrib below sharp, salient, with prickles 2.5–3 mm. long, 10–20 mm. apart, similar, ascending; near the apex the margins and midrib below subulate-serrate, the teeth 0.8–1.2 mm. long, 2–3 mm. apart; peduncle 15 or more cm. long, obtusely trigonous, leafy bracted; syncarp 18 cm. long, 13 cm. in diameter, cylindric but with the ends rounded, of about 92 phalanges, these 4.7–5.1 cm. long, 2.9–3.5 cm. wide, 2.4–2.7 cm. thick, obovoid, when dried reddish brown, 4–6-angled, the sides minutely papillose, gently curving or nearly plane, upper ¼ free, the apex rounded; lateral sutures none; central apical sinuses 2–4 mm. deep, wide V-shaped; carpels 5–12, those of the upper half mostly 6–7, those of the lower mostly 10–11, the central apices oblate-semiorbicular, the marginal ones oblate-pyramidal; stigmas 1–1.8 mm. long, suborbicular to oval, creased, dark, apical, centripetal, mostly oblique; proximal sinus wide, running ½ way to the valley bottom; endocarp median, bony, dark brown except for the pale outer margins, the lateral walls 4–5 mm. thick; seeds 16 mm. long, 4 mm. in diameter, ellipsoid; upper mesocarp in each carpel forming a cavern nearly free of fibers but with pale medullary transverse membranes; basal mesocarp fibrous and fleshy.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Iron Range, occasionally in gullies in rain forest, 20 m. alt., June 24, 1948, *L. J. Brass 19,309* (BRI).

DISCUSSION: The new species is a member of the section *Pandanus*. In this the closest relative seems to be *P. odoratissimus* L. f. var. *novoguineensis* (Martelli) St. John, which as the phalanges 5.7–6 cm. long, 3–3.5 cm. wide, the lateral sinuses distinct in the upper half; apical central sinuses 5–6 mm. deep; carpel apices semiorbicular; and the endocarp supramedian. On the other hand, *P. oblatus* has the phalanges 4.7–5.1 cm. long, 2.9–3.5 cm. wide; lateral sinuses none; apical central sinuses 2–4 mm. deep; apices of the marginal carpels oblate-pyramidal; and the endocarp submedian.

The epithet is the Latin participle, *oblatus*, given the modern scientific meaning, depressed. This refers to the oblate-pyramidal carpel apices.

Pandanus somersetensis sp. nov. (sect. *Pandanus*)
Figs. 29–30

DIAGNOSIS HOLOTYPI: Arbor 5–8 m. alta 20–30 cm. diametro supra media ramosa, cortice armato cum muriculis, radicibus fulturosis 6–15 cm. longis pluribus, foliis 93 cm. longis 6.8–7.2 cm. latis coriaceis glaucis gladiformibus sed sensim diminentibus ad apicem acutum in puncto 10 cm. ex apice 7 mm. latis in base marginibus integris sed ex loco 7–10 cm. e base in uno latere cum aculeis 1.5–2.3 mm. longis 3–8 mm. distantibus crassiter subulatis stramineis adscendentibus sed in latere altero aculeis 0.5–1 mm. longis 3–15 mm. distantibus midnervio exarmato fere ubique, foliis in section mediale integris et in parte apicale marginibus integris sed nervo mediale infra cum aculeis 0.3 mm. longis paucis remotis, pedunculis ca. 25 cm.

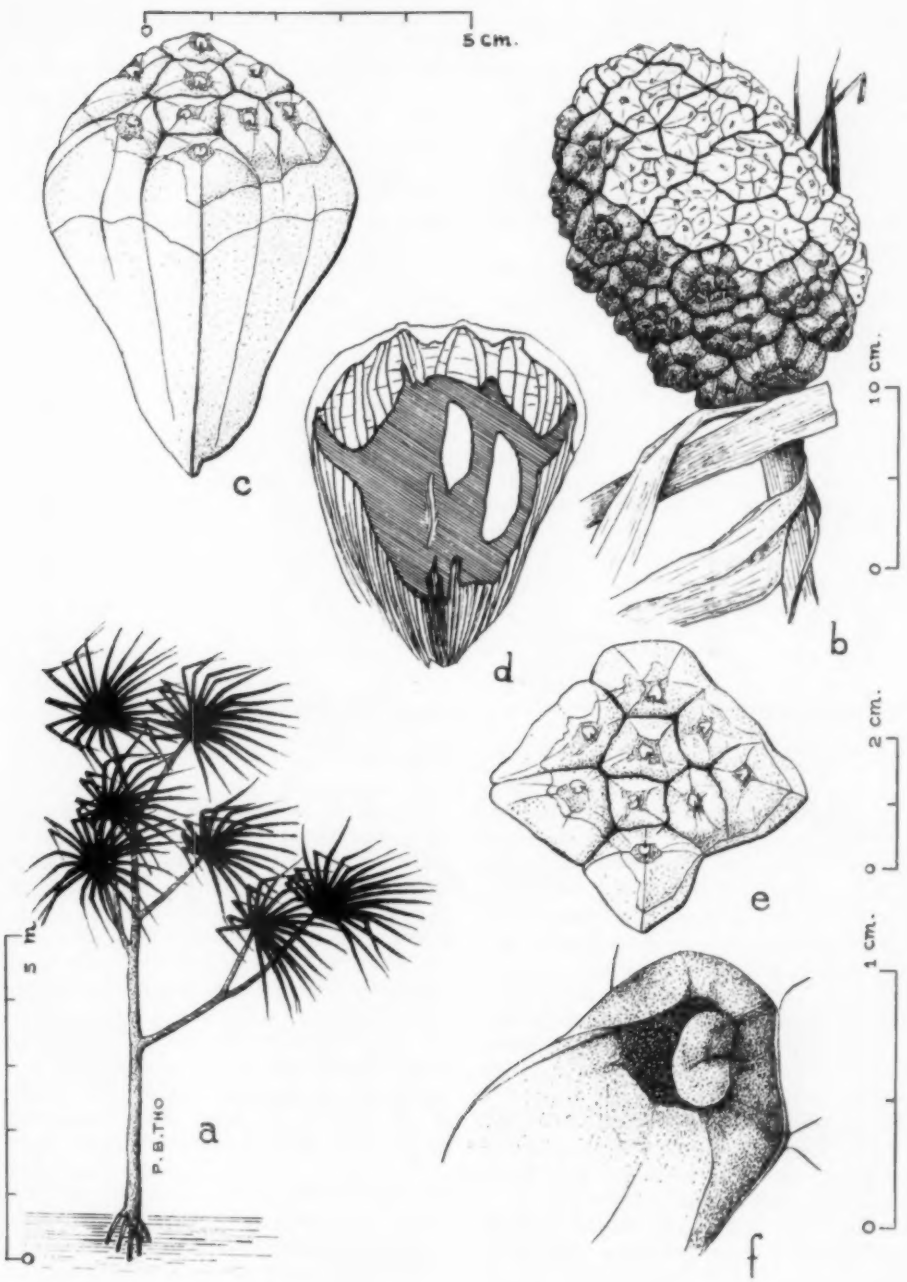

FIG. 29. *Pandanus somersetensis*, from holotype. *a*, Habit, × 1/100; *b*, syncarp, × 3/16; *c*, phalange, lateral view, × 1; *d*, phalange, apical view, × 1; *e*, apex of carpel and stigma, apical view, × 4.

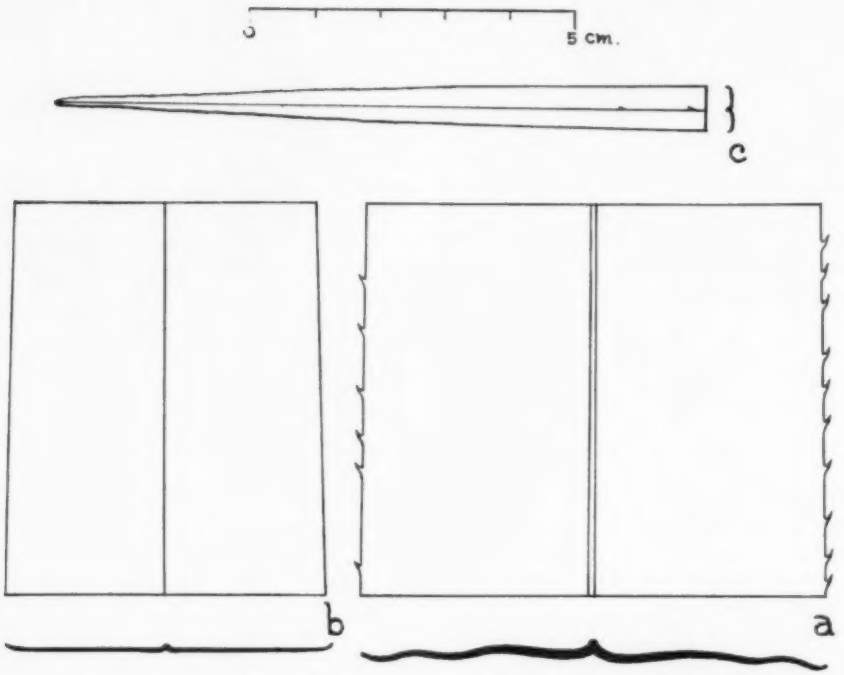

FIG. 30. *Pandanus somersetensis*, from holotype, lower side of leaf, × 1. *a*. Near base; *b*, middle; *c*. apex.

longis foliosis, syncarpiis terminalibus singularibus maximis eorum 22 cm. longis 13 cm. diametro late ellipsoideis subtriangularibus cum ca. 70 phalangibus eis 5–5.5 cm. longis 4–5.1 cm. latis 3.2–4.5 cm. crassis anguste obpyramidalibus 4–6-angulosis in sicco brunneis laevibus et sublucidis lateribus paene curvatis vel planis parte ¼ supera libera, apice lato depresse convexo, suturis lateralibus raris sed paucis et solo in parte quarta supera evidentis, suturis apicalibus centralibus 0.5–1 mm. profundis sed plerumque tam vadosis quam paene imperceptis sunt et suturis solum tessellatis, carpelis 7–9, apicibus inequalibus quod carpelis lateralibus in latere exteriore distentis sunt sed apicibus omnibus veris brunneis subaequalibus et subplanis sed eis centralibus minime depressoconicis, stigmatibus 1.5–3 mm. longis ovatodeltoideis ad ellipticis horizontalibus centripetalibus minime elevatis, sutura proxima ad dimidiam intervallam ad basem producta, endocarpio mediale osseoso subalbo in latere 2–3 mm. crasso, seminibus 15–16 mm. longis 5 mm. diametro oblique ellipsoideis, mesocarpio supero cavernoso et cum fibris longitudinalibus crassis et membranis albis, mesocarpio infero fibroso et carnoso sed minimo.

DIAGNOSIS OF HOLOTYPE: Tree 5–8 m. tall, 20–30 cm. in diameter, branching in 2's or 3's, beginning halfway up, the crown semiorbicular; bark armed with scattered, short, sharp bosses; prop roots several, 6–15 cm. long; leaves 93 cm. long, 6.8–7.2 cm. wide, coriaceous, glaucous, sword-like but tapering gradually from the base to the acute tip, this 10 cm. down 7 mm. wide, at the very base the margins entire, but beginning 7–10.5 cm. above it having on one side ascending prickles 1.5–2.2 mm. long, 3–8 mm. apart, stout subulate, stramineous, but on the other border 0.5–1 mm. long, 3–15 mm. apart, the midrib smooth almost throughout; at the middle the margins entire; near the tip the margins entire and only the midrib below with a few remote ascending prickles 0.3 mm. long;

peduncles about 25 cm. long, leafy bracted; syncarps terminal, single, the largest 22 cm. long, 13 cm. in diameter, broadly ellipsoid, obscurely 3-angled, the color unknown, of about 70 phalanges; phalanges 5–5.5 cm. long, 4–5.1 cm. wide, 3.2–4.5 cm. thick, narrowly obpyramidal, 4–6-angled, when dried light brown, smooth and somewhat shiny, the sides gently curving or plane, free in upper ¼, the apex broad, low convex, lateral carpel sutures mostly none, but a few perceptible down ¼ way, the central apical sutures 0.5–1 mm. deep, but mostly so shallow as to be almost imperceptible and the sutures merely making a tessellate pattern; carpels 7–9, the apices somewhat unequal as the lateral ones have considerable expansion on the outer side, but the brown colored, actual apex is subequal on all and is almost flat, though the central ones have a perceptible depressed conic elevation; stigmas 1.5–3 mm. long, ovate-deltoid to elliptic, horizontal, centripetal, slightly raised, below it the proximal suture on the carpel apex from very short to ½ as long as the distance to the intercarpellary suture; endocarp median, bony, whitish, that surrounding the outer seeds 2–3 mm. thick; seeds 15–16 mm. long, 5 mm. in diameter, obliquely ellipsoid; upper mesocarp cavernous, with very stout longitudinal fibers and delicate, white, medullary membranes; lower mesocarp fibrous and fleshy, but of small extent.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Newcastle Bay, 2½ mi. S. of Somerset, commonly on rocky coastline and beside small freshwater streams in coastal sand dune area, May 13, 1948, *L. J. Brass 18,792* (BRI).

This new species certainly belongs in the section *Pandanus*, even though the stigmas are subhorizontal. None of the published species in that section are so similar that it would be of value to state the contrasting differences.

The new epithet is geographic, indicating the type locality of the species.

Pandanus truncatus sp. nov. (sect. *Pandanus*)
Figs. 31–32

DIAGNOSIS HOLOTYPUS: Arbor 6–8 m. alta, laxe ramosa, foliis 1.43 m. longis 6 cm. latis in base coriaceis ligulatis infra minus glaucis ex base gradatim diminuentibus ad apicem subulatum in puncto 10 cm. ex apice 3 mm. latis in base exarmatis sed ex puncto 15 cm. ex base marginibus cum aculeis 1.5–2 mm. longis 3–10 mm. distantibus aciculatis rectis adscendentibus in apice brunneis, in parte mediale marginibus et midnervio exarmatis, ad apicem marginibus midnervioque infra cum serris remotis 0.2–0.3 mm. longis, syncarpio terminale singulare subpendente, pedunculo 20 cm. longo triangulare bracteato, syncarpio 18 cm. longo 13 cm. diametro late ellipsoideo cum ca. 56 phalangibus 4.5–5 cm. longis 3.1–4.1 cm. latis 2.9–3.3 cm. crassis late obovoideis, apice depresse convexo, ⅓ parte supera libera, lateribus cum 6–8 angulis majoribus et 2–3-plo angulis et vallibus minoribus in sicco pallide brunneis laevibus et lucidis, suturis lateralibus fortibus ½ vel omnia distancia extensis, sinibus centralibus apicalibus 3–4 mm. profundis angustis sinuatisque, carpellis 7–11, apicibus subaequalibus pyramidali-semiorbicularibus omnibus marginalibus et paucis centralibus cum area plana vel minime concava obscure brunnea terminale, stigmatibus centripetalibus 1–1.5 m. longis suborbicularibus vel obcordatis valde inclinatis, sutura proximali et stigmate dimidia vel omnia distancia ad vadum extensa, endocarpio mediale osseoso albo solum in parte supera extensa sed in lateribus et parte infera diminuenda in muris 0.5 mm. crassis, seminibus 23–25 mm. longis 4–6 mm. diametro ellipsoideis, mesocarpio supero pluricavernoso cum fibris validis et membranis medullosis pallidis, mesocarpio infero fibroso et carnoso sed in base toto carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 6–8 m. tall, branched into a very open crown; leaves 1.43 m. long, 6 cm. wide near the base, coriaceous, ligulate, somewhat glaucous below, tapering gradually from the very base up to the subulate tip which 10 cm. down is 3 mm. wide, the base unarmed, but beginning 15 cm. up the margins with spines 1.5–2 mm. long, 3–10 mm. apart, straight acicular, ascending, brown-tipped; in the median region the margins and midrib unarmed; near the apex the margins and midrib below with a few remote serrations 0.2–0.3 mm. long; syncarp terminal, single, almost pendent, borne on a triangular, leafy bracted peduncle about 20 cm. long, the syncarp 18 cm. long, 13 cm. in diameter, broadly ellipsoid, of about 56 phalanges, these 4.5–5 cm. long, 3.1–4.1 cm. wide, 2.9–3.3 cm. thick, broadly obovoid, the

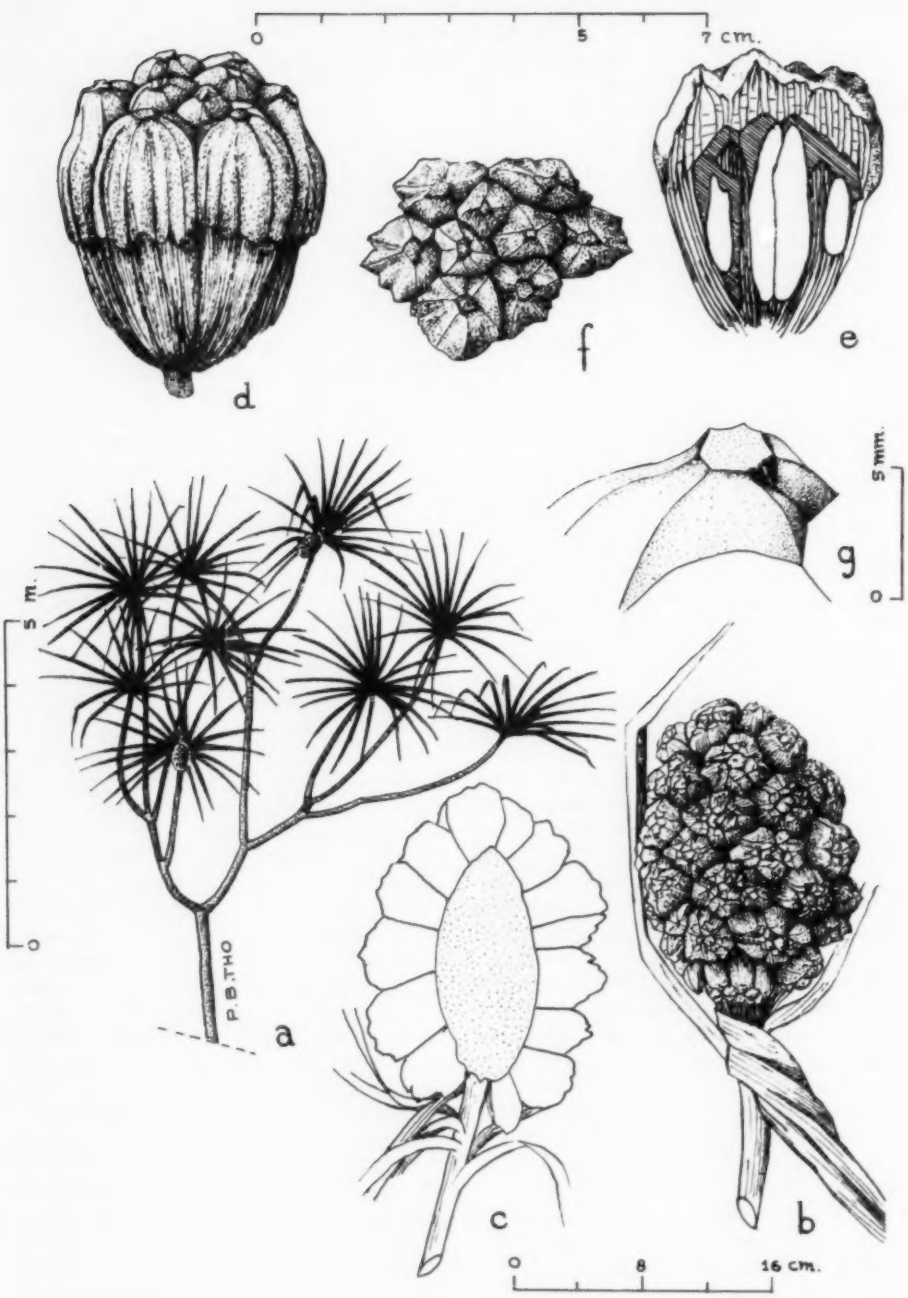

FIG. 31. *Pandanus truncatus*, from holotype. *a*, Habit, × 1/100; *b*, syncarp, × 5/18; *c*, syncarp, longitudinal section, × 5/18; *d*, phalange, lateral view, × 1; *e*, phalange, longitudinal median section, × 1; *f*, phalange, apical view, × 1; *g*, apex of carpel and stigma, oblique view, × 4.

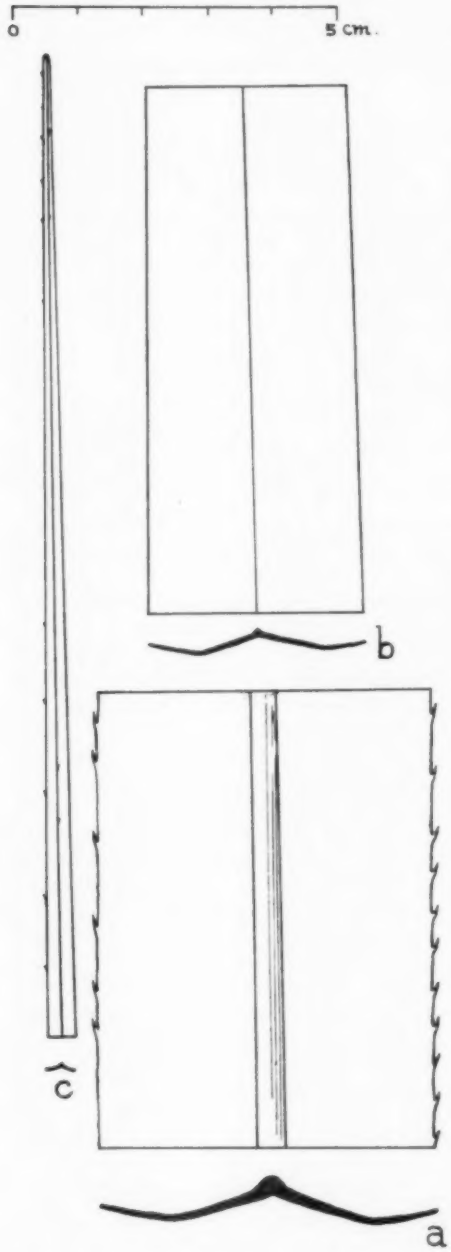

FIG. 32. *Pandanus truncatus*, from holotype, lower side of leaf, × 1. *a*, Near base; *b*, middle; *c*, apex.

apex low convex, upper ⅓ free, the sides with 6–8 major angles and with 2–3-times that number of secondary sharp ridges, so that the adjacent phalanges fit as if mortised, when dried light brown, smooth and shiny, lateral carpel sutures well marked ½ way or nearly all the way down, the central apical sinuses 3–4 mm. deep, the bottoms narrow and sinuous; carpels 7–11, the apices subequal pyramidal-semiorbicular, all the marginal and some of the central ones with a dark brown flat or slightly concave surface below the proximal edge of which is the steeply oblique, centripetal stigma 1–1.5 m. long, suborbicular to obcordate, and below it the proximal crease running ½ way or all the way to the bottom; endocarp median, bony, white, extensive only at the upper end, diminishing on the sides and lower part to thin sheets only 0.5 mm. thick; seeds 23–25 mm. long, 4–6 mm. in diameter, ellipsoid; upper mesocarp of several caverns with strong longitudinal fibers and pale medullary membranes; lower mesocarp fibrous and fleshy, but the actual base almost wholly fleshy.

HOLOTYPUS: Australia, Queensland, Cape York Peninsula, Lockerbie, 10 mi. WSW of Somerset, common and in places forming small groves on sandy soil in savanna-forest, 30 m. alt., 1948, *L. J. Brass 18,552* (BRI).

DISCUSSION: The closest relative, *P. Brookei* Martelli, has the leaves near the base with marginal teeth 2–3 mm. long; syncarp cylindric, 43 × 21.5 cm., with about 66 phalanges the sides of which are plane or gently curving; apices of the marginal carpels broad concave on a broad pyramidal base; central apical sinuses 4–6 mm. deep, the lines straight or gently curved; stigmas horizontal, 2–3 mm. long; and the endocarp 2 cm. long. On the other hand, *P. truncatus* has the leaves with marginal teeth near the base with teeth 1.5–2 mm. long; phalange sides sharply ridged and mortised with neighbors; syncarp broadly ellipsoid, 18 × 13 cm., with about 56 phalanges; apices of marginal carpels with oblique, truncate planes exterior of the stigmas; central apical sinuses 3–4 mm. deep, the lines sinuous; and the stigmas steeply inclined, 1–1.5 mm. long.

The new epithet is the Latin participle, *truncatus*, cut off, or flat ended, in allusion to the shape of the carpel apices.

Revision of the Genus *Pandanus* Stickman, Part 7
New Species from Borneo, Papua, and the Solomon Islands

HAROLD ST. JOHN[1]

THIS SEVENTH PART of the series contains descriptions of miscellaneous new species from islands in the tropical Pacific.

Pandanus Andersonii sp. nov. (sect. *Acrostigma*)

Figs. 33–34

NOM. VERN.: "surong irit."

DIAGNOSIS HOLOTYPI: Pedunculo ad 10 cm. longo 2.5 cm. diametro obtuse trigono ebracteato erecto, syncarpiis 1–3 spicatis in inflorescentia erecta 15 cm. longa evidenta, syncarpiis 11.5–14 cm. longis 13.5–14 cm. diametro late ellipsoideis vel subglobosis obtuse trigonatis cum drupis numerosissimis, drupis 35–40 mm. longis 6–7 mm. latis 5–6 mm. crassis fusiformibus 5–6-angulatis corpore 18–21 mm. longo oblongo-ellipsoideo pileo quam corporem latiore 13–17 mm. longo in stylo sensim diminuenti, parte principali brunnea ex squamis late deltoideis lucidis dense congregatis erectis ex axile perpendicularibus, drupis in fasciculis dehiscentibus, et pileis in laminis grandibus dehiscentibus, stylo 5–7 mm. longo subulato arcuato stigmatam distalem ferento, stigmate 4–5 mm. longo sublineari in fissura, endocarpio in ¼ parte infera albo cartilagineo lateribus 0.2 mm. crassis, mesocarpio apicali cavernoso ellipsoideo 8–9 mm. longo, mesocarpio basali 5 mm. longo fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: "Roots ramify below water table; rhizome at surface level." Stem 20–25 cm. long, 1.2 cm. in diameter, assurgent, forking and forming dense thickets; leaves 2.6–6.8 m. long, 2.6–2.8 cm. wide, coriaceous, ligulate, 3-nerved and plicate, M-shaped in cross section, the under side slightly paler, abruptly narrowed to the heavy subulate tip which 10 cm. down is 13 mm. wide, the base entire and amplexicaul, but beginning 9 cm. up the margins with stout serrations 2–2.5 mm. long, 5–13 mm. apart, pale; the midrib below beginning 7–8 cm. up with reflexed prickles 4–6 mm. long, 7–17 mm. apart, stout arcuate subulate, becoming brown; at midsection the margins with serrations 1–1.5 mm. long, 5–10 mm. apart, pale below, the tips brownish; the midrib unarmed; near the tip the margins and midrib below with serrations 0.5–1 mm. long, the marginal 2–3 mm. apart, those of the midrib 3–8 mm. apart; on the upper side the two secondary ribs with serrations about 0.5 mm. long, 9–30 mm. apart; pistillate inflorescence ascending, not concealed; peduncle up to 10 cm. long, and 2.5 cm. in diameter, obtusely trigonous, bractless, erect; heads solitary or 2–3 in a spike 15 cm. long; syncarps 11.5–14 cm. long, 13.5–14 cm. in diameter, broadly ellipsoid to subglobose, obtusely trigonous, bearing very numerous drupes (several hundred); drupes 35–40 mm. long. 6–7 mm. wide, 5–6 mm. thick, fusiform, 5–6-angled, the body 18–21 mm. long, oblong-ellipsoid; the pileus the widest part, lance conic, 13–17 mm. long, narrowing gradually into the style, the body appearing rough and brown, from the dense outgrowth of closely packed, brown, shining (perhaps viscid) broad triangular scales, erect from the surface and all perpendicular to the drupe axis; drupes shedding in bundles and the pileuses cohering, early shedding in great sheets; style 5–7 mm. long, subulate, arcuate, glabrous, bearing a distal stigma 4–5 mm. long, almost linear in an open crack on the curved style; endocarp in lower ¼, white, cartilaginous, the walls 0.2 mm. thick; apical mesocarp an empty cavern, 8–9 mm. long, ellipsoid; basal mesocarp 5 mm. long, fibrous and fleshy.

HOLOTYPUS: Sarawak, Lawas District, Kayangeran Forest Reserve, in "Sempilor" (*Dacrydium Beccarii* var. *subelatum*) forest, 10 ft. alt., Nov. 1960, *J. A. R. Anderson* (fruit only) (SARF).

[1] Botanist, B. P. Bishop Museum, Honolulu, Hawaii.
Manuscript received September 13, 1960.

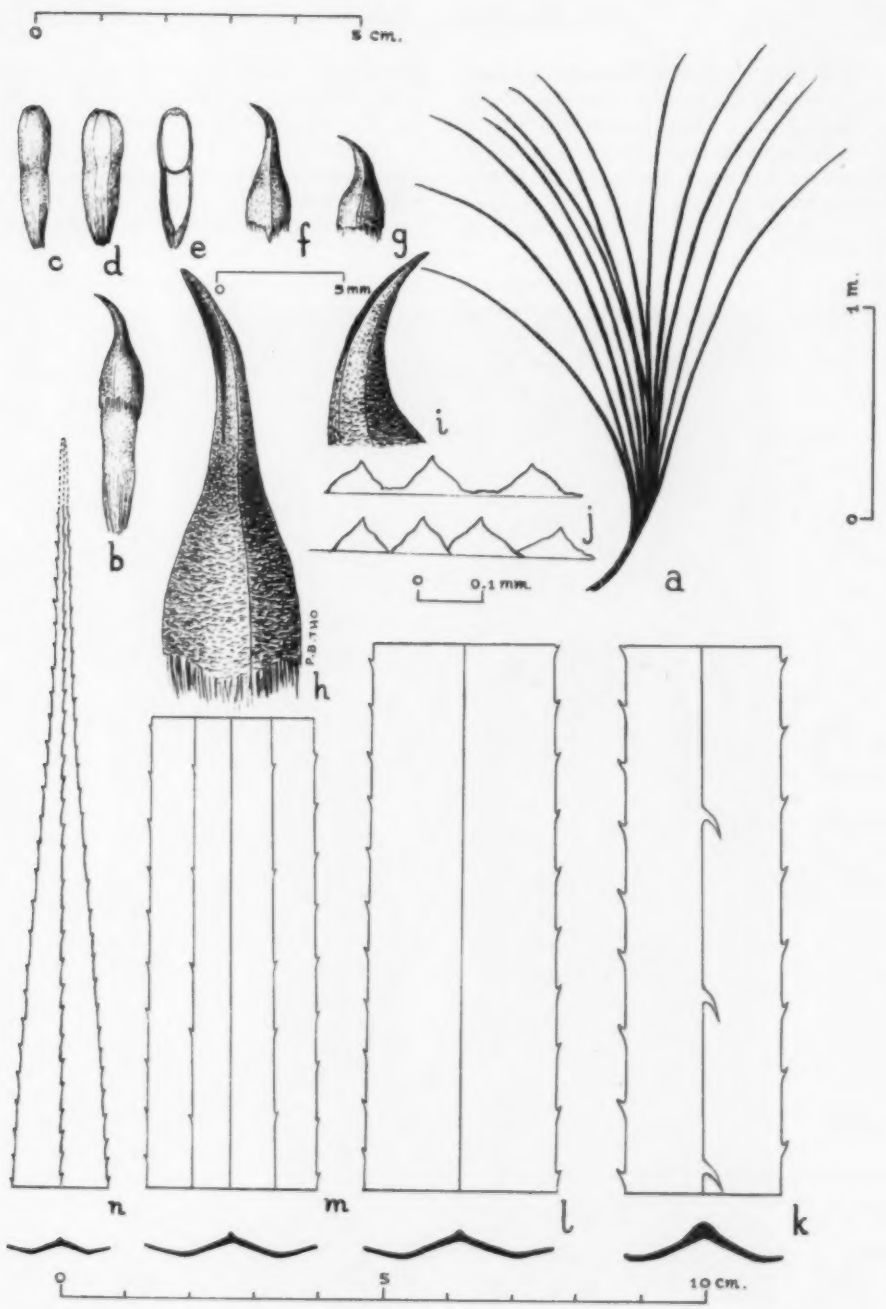

FIG. 33. *Pandanus Andersonii* St. John, from holotype. *a*, Habit, × 1/40; *b*, drupe, lateral view, × 1; *c*, *d*, drupes after shedding pileus, lateral view, × 1; *e*, drupe, longitudinal median section, × 1; *f*, *g*, pileus, lateral view, × 1; *h*, pileus and stigma, lateral view, × 4; *i*, style and stigma of basal drupe, lateral view, × 4; *j*, scales of pileus, basal view, × 100; *k*, base of leaf, lower side, × 1; *l*, leaf middle, lower side, × 1; *m*, leaf, slightly beyond the middle, upper side, × 1; *n*, leaf apex, lower side, × 1.

SPECIMENS EXAMINED: Sarawak, Loba Kabang Protected Forest, abundant, ground flora in "alan" (*Shorea albida*) type forest, found in wetter areas and associated with "bakong" (*Hanguana malayana*), May 16, 1954, *J. A. R. Anderson S.2,815* (SARF).

DISCUSSION: *P. Andersonii* is a member of the section *Acrostigma* and there one finds its closest relative, *P. brevifolius* Martelli of Borneo. This has the syncarp solitary, 5 cm. long, 4 cm. in diameter; drupes 15–16 mm. long, 3 mm. wide; pileus abruptly contracted to the style; and the endocarp in the lower ⅓. On the other hand, *P. Andersonii* St. John has the syncarps

FIG. 34. *Pandanus Andersonii* St. John, in foreground, in peat swamp forest of *Shorea albida*, Baram River, Sarawak. (Photo by J. A. R. Anderson.)

1–3 in a spike and 11.5–14 cm. long, 13.5–14 cm. in diameter; drupes 35–40 mm. long, 6–7 mm. wide; pileus tapering into the style; and the endocarp in the lower ¼.

The new species is named in honor of its collector, Mr. J. A. R. Anderson, Forest Research Officer of the Sarawak government.

Pandanus fruticosus sp. nov. (sect. *Acrostigma*)
Figs. 35–36

DIAGNOSIS HOLOTYPI: Frutex 15.5 m. altus ramosus, ramulis foliosis 6–9 cm. diametro, cortice rubrescenti-brunneo lucido cum cicatricibus pallidis cinctis, foliis 51–58 cm. longis 8–10 mm. latis subcoriaceis ligulatis M-formatis longe diminuentibus in apice subulato 10 cm. ex apice 3.5 mm. lato, marginibus in basi integris sed ex 4 cm. marginibus cum dentibus validis subulatis 0.5–1.3 mm. longis 1–3 mm. distantibus nigris in 45° adscendentibus, midnervio exarmato, marginibus in sectio mediale cum serris nigris 0.5 mm. longis 1–2 mm. distantibus, midnervio infra cum serris nigris 2–6 mm. longis 2–6 mm. distantibus, circa apicem marginibus et midnervio infra cum serris acutis 0.4–0.5 mm. longis 0.5–1.5 mm. distantibus, inflorescentia foeminea solitaria terminale cum bracteis plurimis 16 mm. latis amplectentibus, syncarpio subsessile 3 cm. longo 2 cm. diametro ellipsoideo, drupis multis 9–10 mm. longis 2–2.5 mm. diametro fusiformis, corpore 4–5 mm. longo, pileo obliquiter conico 4 (–5) mm. longo ad stylum tenuato, stylo subulato cum linea stigmata proxima 2.5–3 mm. longa, endocarpio supramediale lateribus 0.1 mm. crassis pallidis, semine 3.5 mm. longo 1.6 mm. diametro late elliptico, mesocarpio infero cavernoso.

DESCRIPTION OF HOLOTYPE: Shrub 15.5 m. tall, forking; leafy branchlets 6–9 cm. in diameter, the bark reddish brown, shining, ringed by pale leaf scars; leaves 51–58 cm. long, 8–10 mm. wide, subcoriaceous, ligulate, M-shaped in cross section, long tapering to a subulate apex which at 10 cm. back from the tip is 3.5 mm. wide, margins at the very base entire, but from about 4 cm. up the margins with stout subulate teeth, 0.5–1.3 mm. long, 1–3 mm. apart, wholly black, ascending at 45°, the midrib unarmed; at the midsection the margins black serrate, the teeth 0.5 mm. long, 1–2 mm. apart, the midrib below appressed, subulate, black serrate, the teeth 2–6 mm. apart; near the apex the margins and midrib below sharply serrate, the teeth 0.4–0.5 mm. long, 0.5–1.5 mm. apart; pistillate inflorescence solitary, terminal, surrounded by several bracteal leaves 16 mm. wide around the spike, but otherwise like the normal foliage leaves; syncarp subsessile 3 cm. long, 2 cm. in diameter, ellipsoid, with numerous drupes; drupes 9–10 mm. long, 2–2.5 mm. in diameter, fusiform, the body 4–5 mm. long, the pileus oblique conic, 4 (–5) mm. long, tapering into the subulate style which is linear stigmatic for 2.5–3 mm. on the proximal side; endocarp from middle to apex of body, the wall 0.1 mm. thick, pale; seed 3.5 mm. long, 1.6 mm. in diameter, broady ellipsoid; lower mesocarp cavernous.

HOLOTYPUS: North Borneo, Keningau District, 76½ mi. on path from Tenom to Ranau (8½ mi. NE. of Tambunan), 2,100 ft. alt., Aug. 27, 1954, *G. H. S. Wood & J. Wyatt-Smith A 4,430* (BRI).

DISCUSSION: The new species *P. fruticosus* is in the section *Acrostigma*. Its nearest relative is the Malayan species *P. aurantiacus* Ridl. which has the leaves 3.8 cm. wide; inflorescence of 5 heads; syncarp 6.2 cm. long, 2.5 cm. in diameter; drupes 18 mm. long; and the endocarp 12 mm. long. On the other hand, *P. fruticosus* has leaves 8–10 mm. wide; the syncarp solitary; drupes 9–10 mm. long; and the endocarp 3.7 mm. long.

The new epithet is the Latin adjective, *fruticosus*, shrubby, given with reference to the plant habit.

Pandanus ruber *sp.* nov. (sect. *Microstigma*)
Figs. 37–38

DIAGNOSIS HOLOTYPI: Arbor 3–5 m. alta ramosa, trunco cum aculeis adscendentibus armato, radicibus fulturosis paucis aculeatis, foliis 172 cm. longis 10.2 cm. latis coriaceis in sectio M-formatis ligulatis acutis in sectio 10 cm. ex apice 4 cm. latis in base integris sed ex puncto 9 cm. e base cum aculeis 1–1.6 mm. longis 2–7 mm. distantibus salientibus stramineis, midnervio inerme, in sectio mediale marginibus cum aculeis 1–1.5 mm. longis 3–6 mm. distanti-

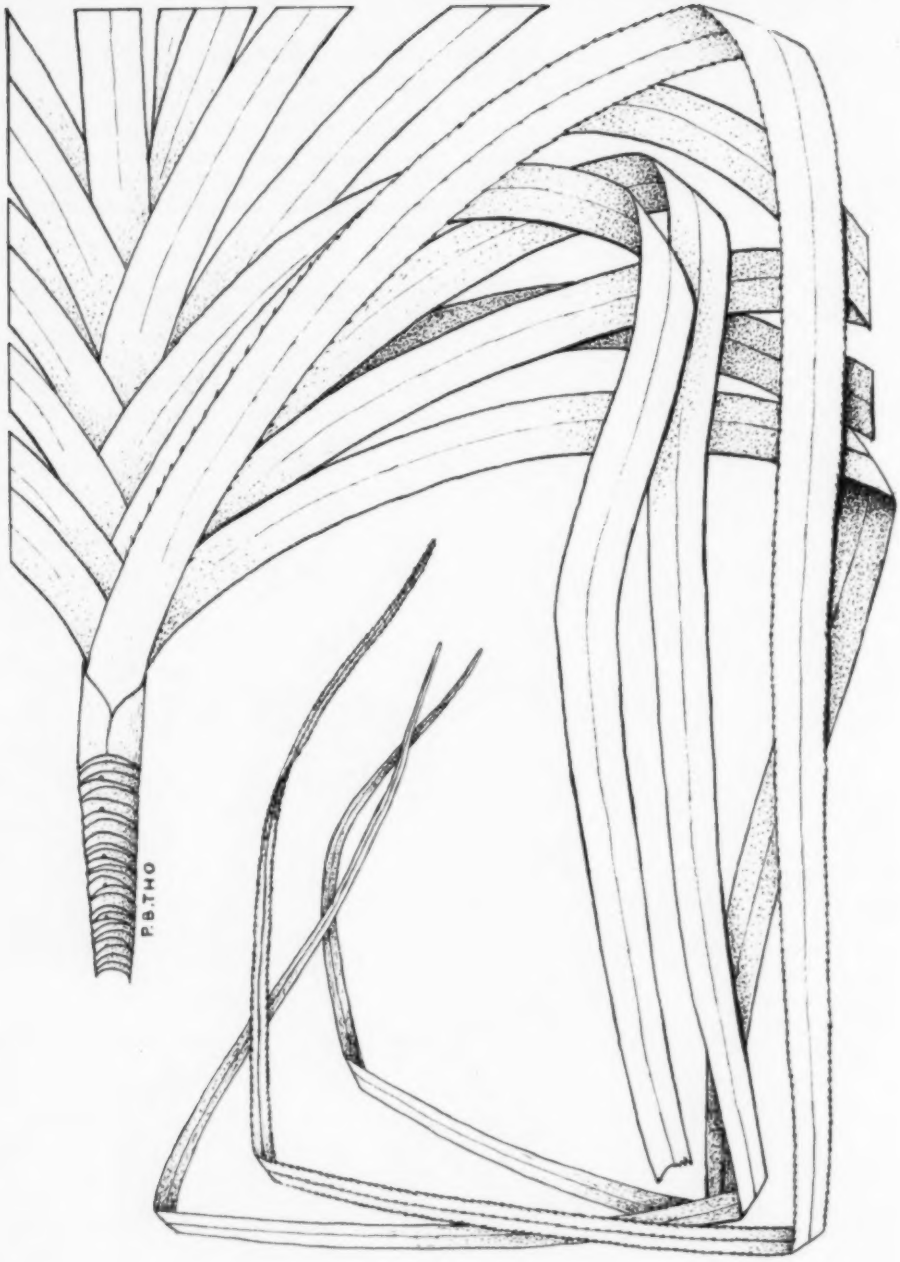

FIG. 35. *Pandanus fruticosus* St. John, from holotype. Habit, × 1.

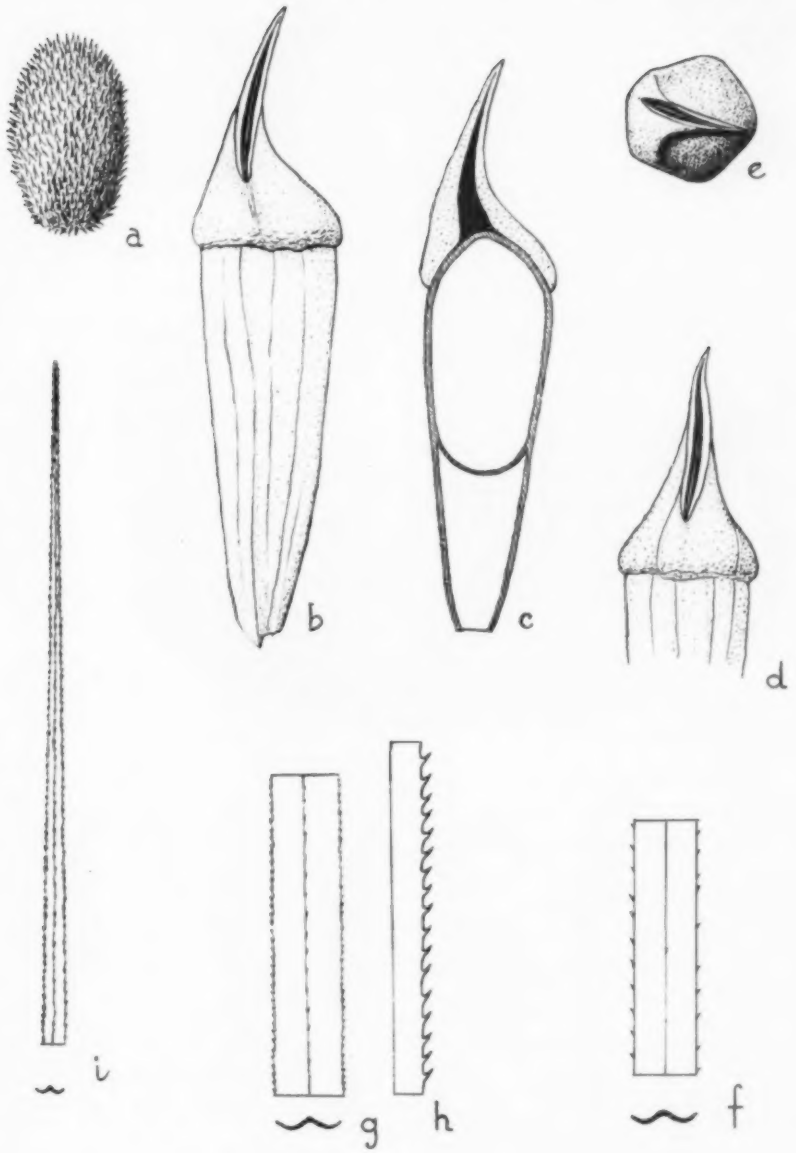

FIG. 36. *Pandanus fruticosus* St. John, from holotype. *a*. Syncarp, lateral view, × 1; *b*. drupe, lateral view, × 10; *c*. drupe, longitudinal median section, × 10; *d*. pileus and stigma, lateral view, × 10; *e*. pileus and stigma, apical view, × 10; *f*. leaf base, lower side, × 1; *g*. leaf middle, lower side, × 1; *h*. leaf margin, at middle, × 10; *i*. leaf apex, lower side, × 1.

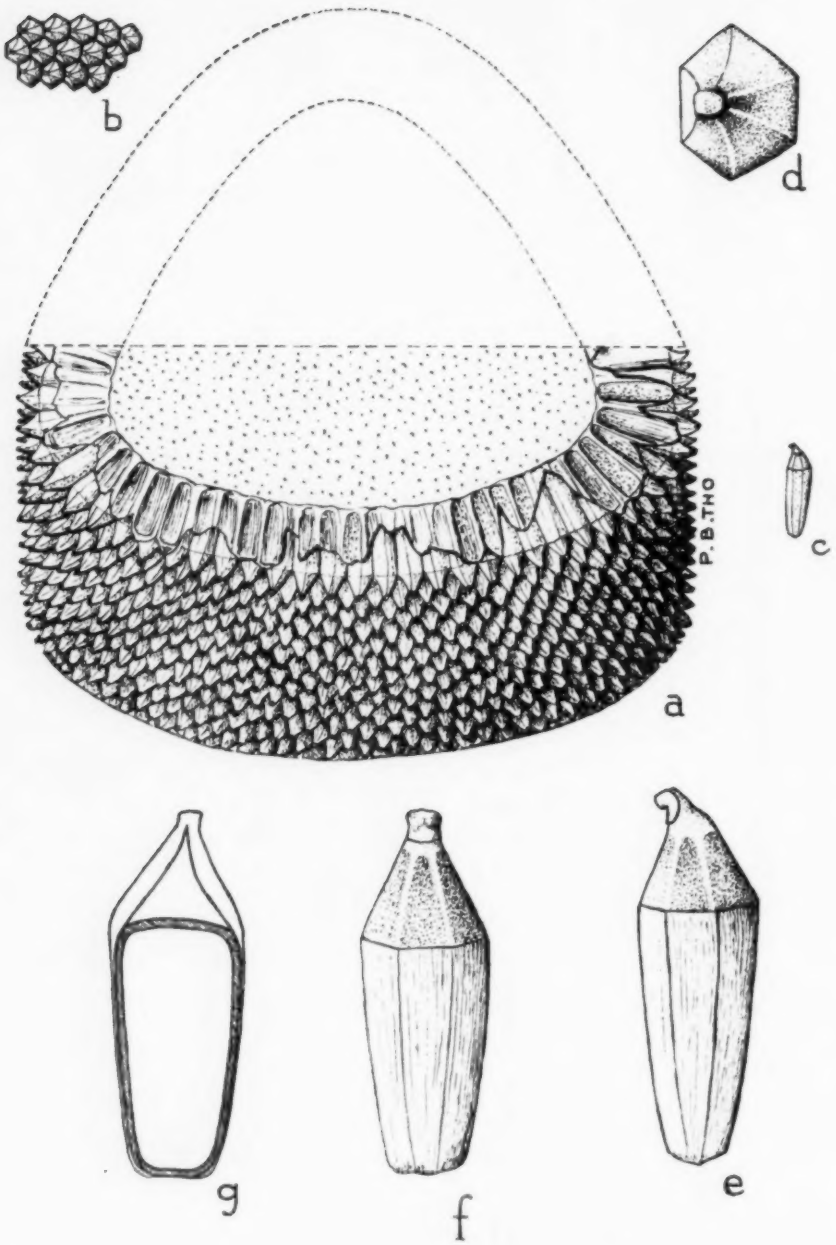

FIG. 37. *Pandanus ruber* St. John, from holotype. *a*. Syncarp, median section, × 1; *b*, drupes, apical view, × 1; *c*. drupe, lateral view, × 1; *d*, drupe, apical view, × 4; *e*. *f*, drupes, lateral view, × 4; *g*. drupe, longitudinal median section, × 4.

bus proxime adpresse-adscendentibus, midnervio cum aculeis 0.3–1 mm. longis 3–11 mm. distantibus valide aciculatis adpresse adscendentibus subbrunneis, proxime apice marginibus unicevel duplo-serratis serris 1.5–2.1 mm. longis 2–5 mm. distantibus stramineis, supra nervis secundariis cum aculeis paucis eis 0.8–1 mm. longis, infra nervo mediale saliente et cum aculeis simultantibus 1.5–2 mm. longis 3–10 mm. distantibus, syncarpiis solitariis plerumque 42 cm. longis 10.5 cm. diametro cylindricis sed subtriangulatis, receptaculo aurantiaco-rubro, drupis numerosissimis in sectio mediale 13–15 mm. longis 3–4.5 mm. latis 2.5–3 mm. crassis unicarpellatis obscure rubris 4–6-angulatis parte ¼ supera libera, pileo 3–4 mm. longo anguste pyramidale asymmetrico et arcuato corpore oblongo in base subcuneato, stigmatibus 0.8–1.5 mm. longis et latis suborbicularibus brunneis verticalibus proximalibus infra petaso terminale, endocarpio basale 9 mm. longo osseoso obscure brunneo lucido 0.4–0.5 mm. crasso, mesocarpio apicale caverno unico.

DIAGNOSIS OF HOLOTYPE: Tree, 3–5 m. tall, branched; trunk and branches armed with upturned prickles; prop roots few, prickly; leaves 172 cm. long, 10.2 cm. wide, coriaceous, M-shaped in cross section, ligulate, acute, 4 cm. wide at 10 cm. from the tip, at the very base the margins entire, but from 9 cm. up prickly, the prickles 1–1.6 mm. long, 2–7 mm. apart, spreading, straw-colored, the nearby midrib unarmed; at the middle point the margins with prickles 1–1.5 mm. long, 3–6 mm. apart, closely appressed ascending, those of the nearby midrib 0.3–1 mm. long, 3–11 mm. apart, stout acicular appressed ascending, brownish near the tip the margin simply or doubly subulate-serrate, the teeth 1.5–2.1 mm. long, 2–5 mm. apart, straw-colored, above the ribs of the two secondary pleats with a few ascending prickles 0.8–1 mm. long, below the salient midrib with similar prickles 1.5–2 mm. long, 3–10 mm. apart; syncarps solitary, averaging 42 cm. long, 10.5 cm. in diameter, cylindric but somewhat 3-sided; receptacle, orange-red; with myriad drupes, those at midsection 13–15 mm. long, 3–4.5 mm. wide, 2.5–3 mm. thick, 1-celled, dark red, 4–6-angled, upper ¼ free, the pileus 3–4 mm. long, narrowly pyramidal, asymmetric and arcuate to the apex, body almost oblong, but slightly cuneate below; stigmas 0.8–1.5 mm. long and wide, suborbicular, brown, vertical on proximal side of apex, below the apical cap; endocarp basal, 9 mm. long, bony, dark brown, shiny, the walls 0.4–0.5 mm. thick; apical mesocarp a single cavern.

HOLOTYPUS: Papua, Central Division, Bella Vista, 1,450 m. alt., planted by the natives in gullies and ravines close to their gardens, Nov. 1933, *L. J. Brass 5,463* (BRI); and isotype (A).

DISCUSSION: The closest relative is *P. Hollrungii* Warb. of Deutsch Neu-Guinea, now Australian New Guinea. It differs by having: the leaves 2.5 m. long, 5 cm. wide; syncarp 35 × 4–7 cm., sessile, spathe-surrounded; drupes 11–13 mm. long, 2.5–3 mm. wide, the apex semi-orbicular-pyramidal; stigmas apical, subhorizontal, 1.5 mm. wide; and the endocarp slightly submedian. *P. ruber* differs by having: the leaves 1.7 m. long, 10.2 cm. wide; syncarp 42 × 10.5 cm.; drupes 13–15 mm. long, 3–4 mm. wide, 3 mm. thick, the apex narrowly pyramidal, asymmetric and arcuate; stigmas 0.8–1.5 mm. wide, vertical on proximal side below overhanging apical cap; and the endocarp basal.

The collector recorded that, "the leaves of mature trees always much damaged by insects...." Also that the trees were cultivated. It is doubtless also wild in the forest. The several similar species with cylindric, red syncarps yield on boiling a fruit sauce important in the diet of the New Guinea natives.

This plant was identified as *P. conoideus* Lam. by Merrill and Perry (Journ. Arn. Arb. 20: 175, 1939). Lamarck's species is similar in its subterminal stigmas, but the drupes are 16 mm. long, the pileus is broader, and the endocarp is only submedia, and the leaves are narrower and with horrid spines. It is based on *P. ceramicus* Rumph (1743) from Amboina, Ceram, and the Indonesian islands.

The epithet, *ruber*, is the Latin adjective meaning red, here chosen because of the red color of the fruits.

Pandanus yuleensis sp. nov. (sect. *Pandanus*)
Figs. 39–40

DIAGNOSIS HOLOTYPI: Frutex ad 6.6 m. alta, cortice radicibus crassis adscendentibus ad 12

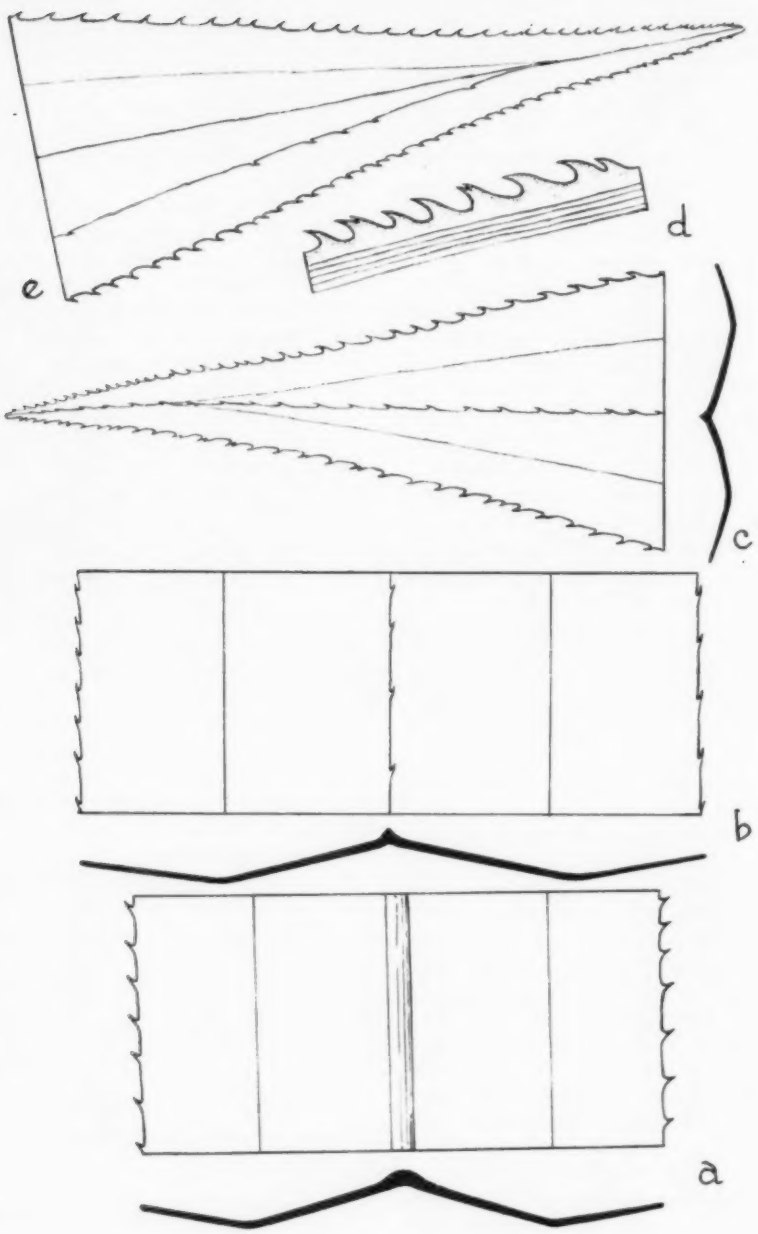

FIG. 38. *Pandanus ruber* St. John, from holotype. *a*, Leaf base, lower side, × 1; *b*, leaf middle, lower side, × 1; *c*, leaf apex, lower side, × 1; *d*, leaf margin, near apex, × 3; *e*, leaf apex, upper side, × 1.

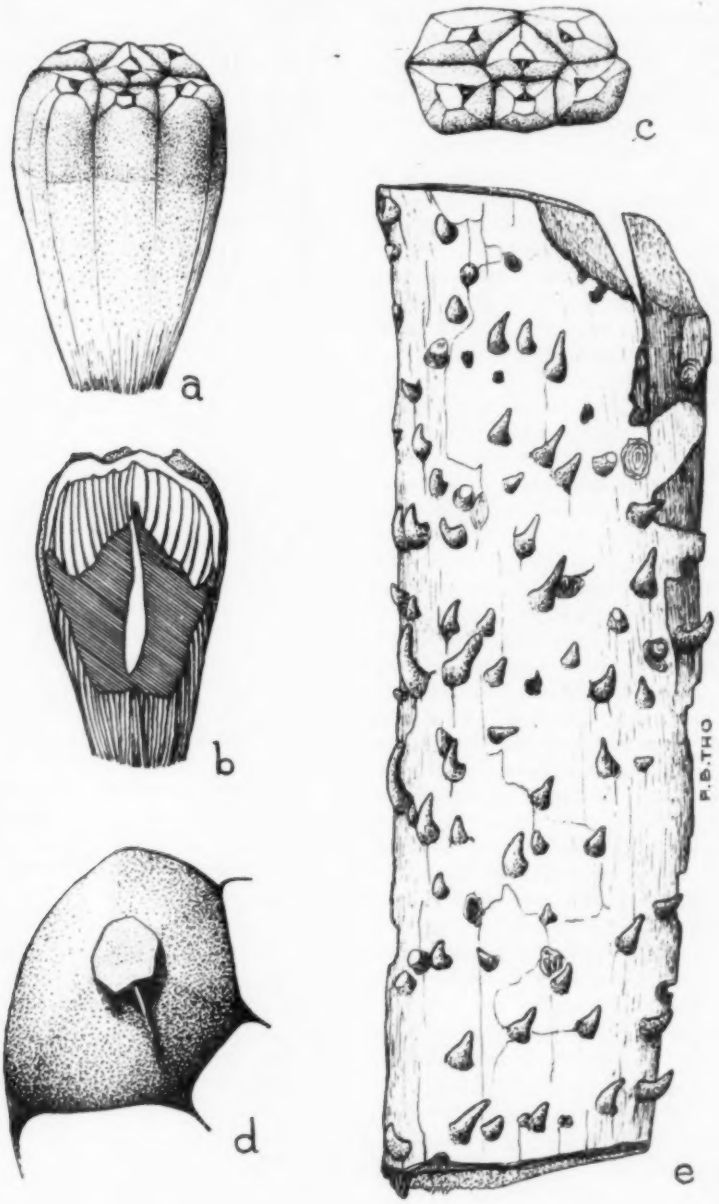

FIG. 39. *Pandanus yuleensis* St. John, from holotype. *a*. Phalange, lateral view, × 1; *b*. phalange, longitudinal median view, × 1; *c*. phalange, apical view, × 1; *d*. carpel, apical view, × 3; *e*. stem with ascending rootlets, lateral view, × 1.

mm. longis 3–10 mm. distantibus obtectis, foliis 1.6 m, longis 5.3 cm. latis gladiformis vel ligulatis sed paulatim ex base in apice longo subulato diminuentibus coriaceis in sectio transverso late M-formatis griseo-viridibus infra apparente glaucis apice deltoideo et 10 cm. ex puncto 1 mm. lato in base marginibus integris sed ex puncto 16 cm. e base cum dentibus 1.5–2 mm. longis 3–12 mm. distantibus subulatis paene curvatis in base brunneis midnervio inerme, in medio in uno latere cum dentibus 1–1.5 mm. longis 3–15 mm. distantibus adpresse adscendentibus in puncto brunneis, latere altero inerme, midnervio infra cum dentibus 0.3 mm. longis 10–30 mm. distantibus paucis brunneis validis subulatis adpresse adscendentibus, ad apicem marginibus midnervioque infra cum serris paucis 0.2 mm. longis remotis brunneis, syncarpiis scilicet terminalibus solitariisque griseo-viridibus ad 12.5 cm. diametro, phalangibus 4.4–4.7 cm. longis 2.2–3 cm. latis 1.9–2 cm. crassis late cuneatis apice subconvexo vel truncato compressis parte ⅓ supera libera lateribus 5–6-angulosis subcurvatis vel paene planis laevibus lucidis in sicco brunneis, suturis lateralibus nullis, sinibus apicalibus centralibus 3–3.5 mm. profundis, carpellis 4–6 apicibus subaequalibus conico-suborbicularibus eis marginalibus plerumque cum petaso truncato parvo et sub margine proximo eo stigma est, stigmatibus 1–2 mm. longis ovalibus vel obdeltoideis sillonatis centripetalibus, sutura proxima ex stigmate dimidia vel omnina distancia ad vadum extento, endocarpio mediale 25–27 mm. longo osseoso obscure brunneo lateribus 2.5–8 mm. crassis, seminibus 15–20 mm. longis 4 mm. diametro, mesocarpio apicale cavernoso cum fibris longitudinalibus et membranis medullosis, mesocarpio basale fibroso et carnoso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree up to 6.6 m. tall; bark gray, with abundant ascending, stout, adventitious roots up to 12 mm. in length but having no further development, placed 3–10 mm. apart; leaves 1.6–1.96 m. long, 5.3–6 cm. wide, sword-shaped or ligulate but tapering gradually from the base to the long subulate tip, coriaceous, in section broad M-shaped, gray-green, below apparently somewhat glaucous, the apex triangular and 10 cm. back only 1 mm. wide, at base the margins entire, but

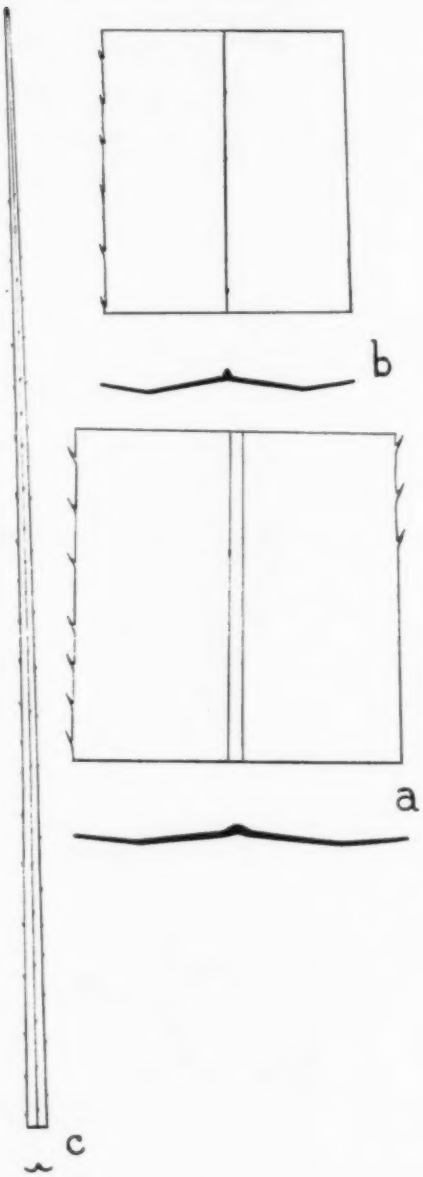

FIG. 40. *Pandanus yuleensis* St. John, from holotype. *a*. Leaf base, lower side, × 1; *b*. leaf middle, lower side, × 1; *c*. leaf apex, lower side, × 1.

beginning 10–16 cm. up, with teeth 1.5–2 mm. long, 3–12 mm. apart, subulate, gently curved, brown based, the midrib unarmed; at the middle with teeth on one side 1–1.5 mm. long, 3–15 mm. apart, brown tipped, subulate, appressed ascending, but the other margin unarmed, the adjacent midrib below with a few teeth 0.3 mm. long, 10–30 mm. apart, brown, stout subulate, appressed ascending; near the apex the margins and midrib below with a few, remote, brown serrations 0.2 mm. long; syncarps probably terminal and solitary, "gray green, up to 12.5 cm. in diameter," phalanges 4.4–4.7 cm. long, 2.2–3 cm. wide, 1.9–2 cm. thick, broad cuneate, the apex subconvex or truncate, compressed, upper ⅓ free, the sides 5–6-angled, gently curving or nearly plane, smooth, shining, when dried brown, lateral carpel sutures none, central apical sinuses 3–3.5 mm. deep; carpels 4–6, the apices subequal, conic-semiorbicular, the marginal ones usually with a small truncate cap in the proximal lee of which is the inclined stigma, stigmas 1–2 mm. long, oval to obdeltoid, creased, centripetal, below it the proximal crease on the carpel apex running from half way to all the way to the bottom; endocarp median, 25–27 mm. long, bony, dark brown, the lateral walls 2.5–8 mm. thick; seeds 15–20 mm. long, 4 mm. in diameter; apical mesocarp cavernous, traversed by longitudinal fibers and with delicate medullary membranes; basal mesocarp fibrous and fleshy.

Papua: Yule Island, Jan. 16, 1955, *J. S. Womersley & N. W. Simmonds 5,099* (BRI).

SPECIMENS EXAMINED: Papua, Yule I., July/Aug., 1918, *C. T. White 770* (BRI), consisting of one leaf only.

DISCUSSION: The most similar kind is *P. odoratissimus* L. f. var. *novo-caledonicus* (Martelli) St. John, which has the phalanges 5.5 cm. long, the upper half free; carpels 7–9, the outer 2–3-times the larger; apical central sinuses 2–3.5 mm. deep; stigmas apical, horizontal; and the endocarp ⅓ the length of the phalange. On the contrary, *P. yuleensis* has the phalanges 4.4–4.7 cm. long, the upper third free; carpels 4–6, subequal; apical central sinuses 3–3.5 mm. deep; stigmas steeply oblique, placed below the truncate apex; and the endocarp more than half the length of the phalange.

The new specific epithet is an adjective made from the name of the type locality, Yule, by adding the Latin place suffix, *-ensis*.

Pandanus magnicavernosus sp. nov. (sect. *Mammillarisia*)

Figs. 41–42

DIAGNOSIS HOLOTYPI: Arbor 8 m. alta erecta ramosa cum radicibus fulturosis, foliis 1.8–1.9 m. longis 9.5–10 cm. latis pallide viridibus molliter subcoriaceis subplanis in base midnervioque luteo-brunneis midnervio et nervis binis secundariis fortibus sed dentis innoxis apice acuto base paene dilatata et cum marginibus membranaceis per 25 cm. inermibus, marginibus ultra cum serris fortibus 1.5–2 mm. longis 3–10 mm. distantibus stramineis sed apicibus brunneis, midnervio inerme, in sectio mediale marginibus cum serris 0.5 mm. longis 2–10 mm. distantibus subulatis valde adpressis, midnervio infra cum aculeis simulantibus subulatis sed fortioribus et paene brevioribus, nervis secundariis inermibus, ad apicem marginibus cum serris subulatis 0.5–0.9 mm. longis 1–2 mm. distantibus pallidis adscendente adpressis, nervis secundariis supra scabris cum serris minutis irregularibus adscendentibus, midnervio infra cum aculeis 0.3–1 mm. longis subulatis adscendentibus aggregatis, pedunculis 90 cm. longis gracilibus triangularibus, syncarpio solitario penduloso 24 cm. diametro globoso glauco, phalangibus 2–3 (rare 1)-carpellatis numerosis 7.5–8.5 cm. longis 17–35 mm. latis 14–21 mm. crassis cuneiformis 5–7-angulosis carnosis parte supera 1/6 libera apice depresse conico plurianguloso cum 1–3 extremitatibus, sinibus apicalibus centralibus 1–2 mm. profundis, stigmatibus 1.5–2 mm. longis cordatis apicalibus sulcatis quando binis centripetalibus quando tribus eo centrali ad laterem dirigito, lateribus phalangiorum planis, endocarpio in tertia infera 24–30 mm. longo osseoso pallide brunneo lateribus 3–4 mm. crassis, seminibus 10–12 mm. longis 3–4 mm. diametro ellipsoideis, mesocarpio supero cavernam unical dimidiam quam longam quam syncarpiam formante sed sectio breve cum fibris et membranis medullosis, mesocarpio infero fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: "Tree, 8 m. tall, erect, branched near top; trunk supported on

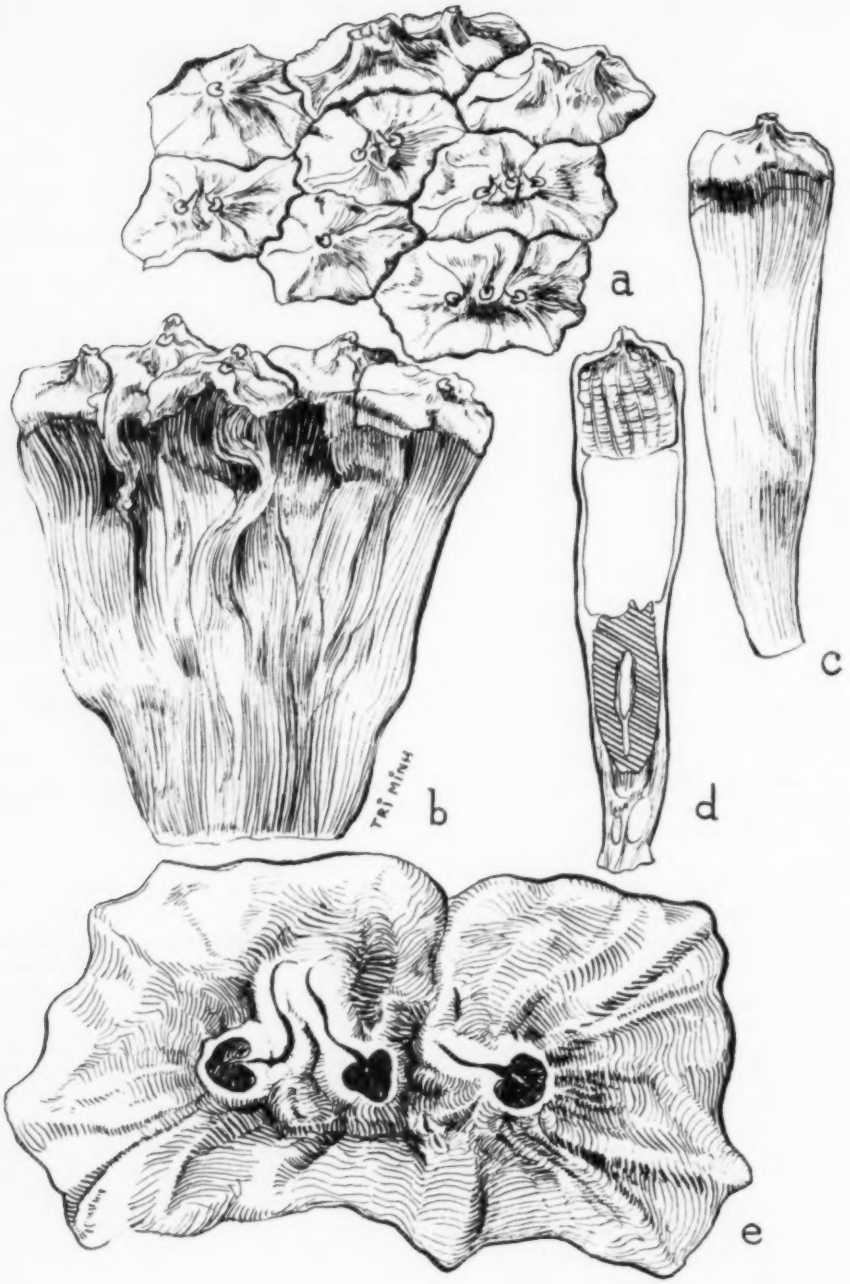

FIG. 41. *Pandanus magnicavernosus* St. John, from holotype. *a.* Phalanges, apical view, × 1; *b.* phalanges, lateral view, × 1; *c.* phalange, lateral view, × 1; *d.* phalange, longitudinal median section, × 1; *e.* phalange and stigmas, apical view, × 4.

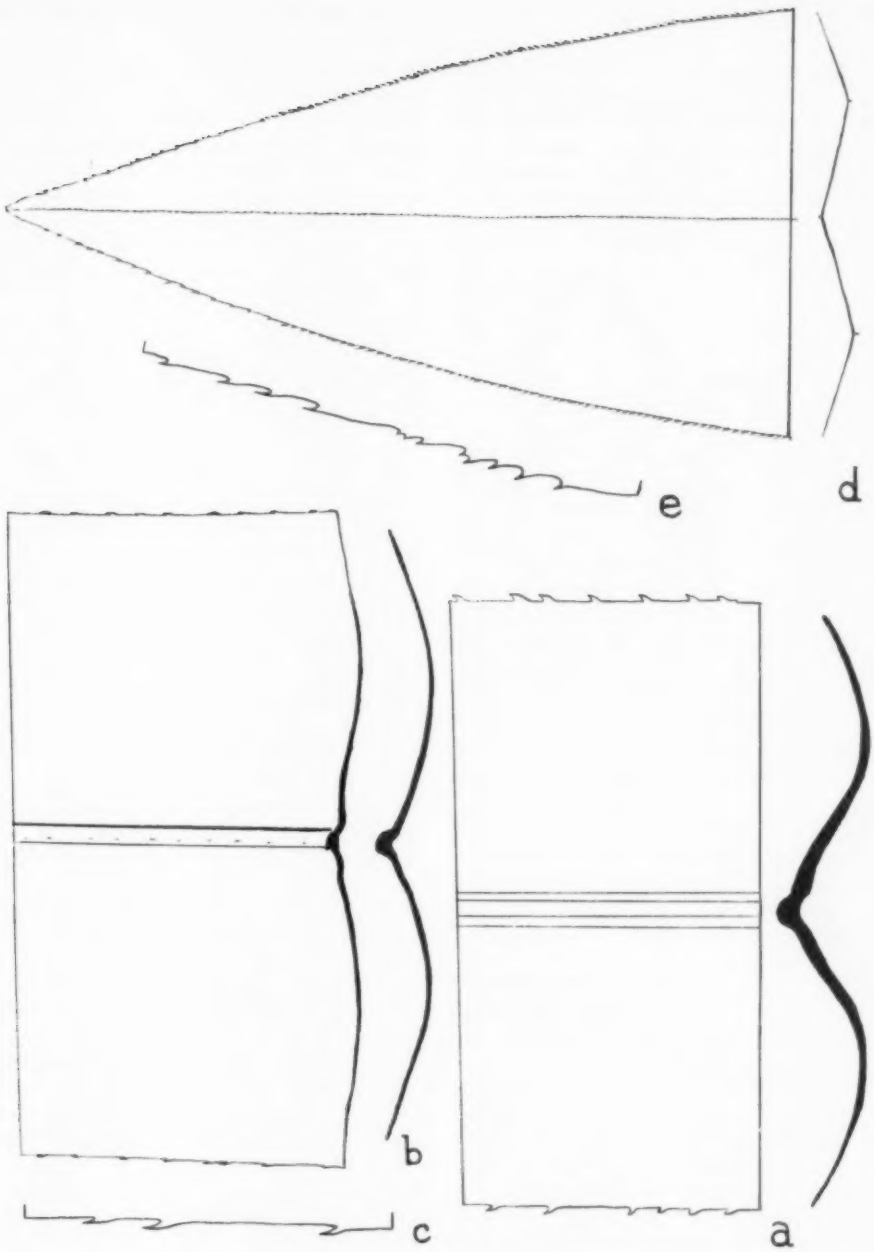

FIG. 42. *Pandanus magnicavernosus* St. John, from holotype. *a*, Leaf base, lower side, × 1; *b*, leaf middle, lower side, × 1; *c*, leaf margin at middle, × 4; *d*, leaf apex, lower side, × 1; *e*, leaf margin near apex, × 4.

stilt roots; leaves 1.8–1.9 m. long, 9.5–10 cm. wide, pale green, glaucous beneath, midrib and basal part of leaf yellow brown," soft coriaceous, nearly flat, the midrib and two secondary ribs strong, the teeth inoffensive, the apex abruptly acute, the base slightly dilated and with a membranous unarmed margin for 25 cm., beyond that the margins with stout serrations 1.5–2 mm. long, 3–10 mm. apart, stramineous but brown tipped, the adjacent midrib unarmed; the margins at midsection with the teeth 0.5 mm. long, 2–10 mm. apart, subulate but closely appressed, the midrib below with similar but stouter and slightly shorter subulate prickles, the secondaries unarmed; near the tip the margins with subulate prickles 0.5–0.9 mm. long, 1–2 mm. apart, ascending-appressed, pale, the secondaries above scabrous with minute, irregular, ascending serrations, below the midrib crowded with ascending subulate prickles 0.3–1 mm. long; fruit on slender 3-angled peduncle 90 cm. long; syncarp solitary, pendulous, 24 cm. in diameter, globose, glaucous; phalanges 2–3 (rarely 1)-celled, numerous, 7.5–8.5 cm. long, 17–35 mm. wide, 14–21 mm. thick, wedge-shaped, 5–7-angled, fleshy, upper 1/6 free, the apex depressed conic, with 1–3 tips, several angled, apical central sinuses 1–2 mm. deep and the crease between adjacent phalanges narrow, 1 mm. deep; stigmas 1.5–2 mm. long, cordate, apical, creased, if two then centripetal, if three then the central one facing laterally, phalange sides plane; endocarp in lower third, 24–30 mm. long, bony, pale brown, the lateral walls 3–4 mm. thick; seeds 10–12 mm. long, 3–4 mm. in diameter, ellipsoid; upper mesocarp one huge cavern occupying upper half of phalange except a short apical part with longitudinal fibers and transverse medullary membranes; lower mesocarp fibrous and fleshy.

HOLOTYPUS: Solomon Islands, San Cristoval I., Star Harbour, rain forest on coastal hills, one tree seen, Oct. 28, 1932, *L. J. Brass 3,120* (BRI).

DISCUSSION: This is a striking tree, with ample leaves and huge, conspicuous fruits. It fits into the section *Mammillarisia*, but at present has no known close relatives.

The specific epithet is formed from the Latin, *magnus*, large; *cavernosus*, cavernous, in allusion to the cavernous upper mesocarp.

Feral Rabbit Populations on Pacific Islands

J. S. WATSON[1]

IN THEIR MONOGRAPH, Thompson and Worden (1956: 7–22) discuss the world distribution of the European rabbit (*Oryctolagus cuniculus* L.), but make no mention of several colonies established on islands of the tropical and subtropical Pacific. It is worth drawing attention to these both to complete the picture and because of the light they throw on the great adaptability of this species.

LAYSAN ISLAND (25° 46′ N.; 171° 49′ W.): A low, sand and coral island about 2 mi. long by 1 mi. wide, in the northern half of the Hawaiian chain. Groves of sandalwood trees, thickets of bushes, and fan palms formerly grew on the island, which supported a vast albatross rookery and five endemic species of land birds. The guano deposits of Laysan were exploited between 1892 and 1904, and the manager of the works, Mr. M. Schlemmer, introduced various breeds of domestic rabbits, including the large white domestic English rabbit, to the island in about 1903 (Dill and Bryan, 1912; E. H. Bryan, 1942). The island was later set aside as a bird sanctuary. Professor Homer R. Dill led a scientific expedition from Iowa State College to Laysan in 1911. The expedition found that although the rabbits had killed many bushes and nearly exterminated several plant species, they had on the whole done less damage than might have been expected from their numbers. The extermination of the rabbits, however, was recommended as they were likely to eat out the vegetation which would result in the disappearance of the insects on which a number of endemic bird species were dependent (Dill and Bryan, 1912). To accomplish this an expedition of four men was sent to the island for 3 months in 1912–13; unfortunately, they were inadequately equipped to deal with the problem and, although over 5,000 rabbits were shot, there were so many petrel burrows and other cover that without poison it was impossible to eliminate them in so short a time (Bailey, 1956). In 1923 the Tanager Expedition visited Laysan; the island by then had been reduced to a barren waste of sand with a few stunted trees, only 4 of the 26 species of plants recorded from the island were found (Christophersen and Caum, 1931); and there were a few hundred rabbits present. These were shot, the last ones being hunted out individually. The endemic warbler (*Acrocephalus familiaris* Rothschild) had vanished; the last three Laysan honeyeaters (*Himatione sanguinea fraithii* Rothschild) died during a sand storm while the expedition was on the island; and the Laysan rail (*Porzanula palmeri* Frohawk) died out shortly afterwards (Wetmore, 1925). Extermination of the rabbits was completed and no sign of them was seen in 1936, when the island was found to be recovered in vegetation. While circling over Laysan in an aeroplane in 1949, Bailey (1956) found that the vegetation had staged a remarkable recovery and there were concentrations of black-footed albatrosses (*Diomedea nigripes* Forster) and Laysan albatrosses (*D. immutabilis* Rothschild).

LISIANSKI ISLAND (26° N., 174° W.): Another low sand and coral island about 1¼ mi. long by ¾ mi. wide, in the Hawaiian chain, some 115 mi. west of Laysan. Rabbits from Laysan liberated there some time after their introduction on Laysan in 1903 had destroyed the vegetation by 1913, when only a few living but many dead rabbits were seen (Elschner, 1915). When the Tanager Expedition arrived in 1923 the only signs of rabbits were their bleached and weathered bones, and the vegetation was starting to come back. The rabbits, having stripped the vegetation, had apparently died of starvation (Wetmore, 1925).

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J. S. Watson died August 12, 1959, after completing the first draft of this paper. Additional information on rabbits in the Hawaiian Islands has since been obtained and included in the text.—K. Wodzicki.

ISLETS IN MAIN HAWAIIAN GROUP: According to Mr. D. N. Woodside (personal communication), rabbits were introduced to several of the small islets of volcanic origin (10 to 70 acres) lying off the islands of the main Hawaiian group at unrecorded dates before or about 1915. At present only three of the islets are populated by rabbits: Manana ("Rabbit Island") (22° N., 158° W.), off the coast of Oahu; Lehua (22° N., 160° W.), off the coast of Niihau; and Molokini (21° N., 156° W.), situated in the channel between Maui and Kahoolawe. These tuff-cone islets are rather arid, suffering summer drought and occasionally missing sufficient winter rains to alleviate the dryness. The rabbit populations are subject to violent fluctuations, "die-offs" occurring during the droughts, which perhaps enables the vegetation to survive. There are no predators on these islets. The rabbits on Lehua and Molokini appear to be a mixture of domestic breeds, being of every colour; the Manana rabbits closely resemble the American cottontail in colour and ear length and it is conceivable that these rabbits are in fact cottontails (*Sylvilagus* spp.).

PHOENIX ISLAND (4° S., 171° W.): A small coral island about ¾ mi. long in the Phoenix group. There was an American guano company working here in the late 1860's and about this time domestic rabbits were liberated (Bryan, 1942). Lister (1891) found them fairly plentiful in 1889 and they were still fairly numerous in 1924, but apparently were doing no damage to the vegetation (Bryan, 1942). A survey party, which in 1937 caught a number of rabbits there in an unsuccessful attempt to liberate them in the Gilbert Islands, found them in very poor condition, squatting and allowing themselves to be caught after running about a hundred yards. There is no fresh water on the island (Maude and Maude, 1952).

PHILLIP ISLAND: A small island about half a mile long of decomposed basalt rising to 900 ft., lying off Norfolk Island (29° S., 168° E.), originally covered with trees and thick vegetation. Pigs which were introduced at an early date destroyed much of the undergrowth and rooted up the soil, starting erosion. Rabbits were introduced subsequently (Laing, 1915) and the island thronged with them in 1865 and their principal food seemed to be the bark of trees (Brenchley, 1873). By 1912 the island was fast becoming a complete desert; there was practically no soil, only a few isolated trees; hardly a seedling was to be seen and the only grass was in clefts in the rock near the beach (Laing, 1915). Rabbits were still present in 1943 and a single tree was conspicuous in its isolation (Mr. I. L. Baumgart, personal communication).

The present situation on Phillip Island is indicated in a recent letter to Dr. K. Wodzicki from Mr. B. a'B Marsh, Agricultural Officer, Norfolk Island.

Mr. Marsh made a hurried visit to the island on 4 March 1961 and saw rabbit scratchings, droppings, and a few burrows, the last being under the roots of *Lagunaria Patersonii* and another unidentified tree. The visit, being in the middle of the day, was not well timed for seeing rabbits, but, as a very rough guess, Mr. Marsh thought there might be between two and four dozen rabbits on the island. The animals had been eating the leaves of *Lagunaria* which seemed their main food.

Vegetation consists of six Norfolk Island pines (*Araucaria excelsa*), several dozen *Lagunaria* trees, a few unidentified trees with large shiny leaves, a reed known locally as Mo-oo and a few grasses and weeds. The reed grows in a few areas of 1/10 to ½ acre, usually in flat areas where there is enough soil to retain water, but over perhaps 80 per cent of the island there is no vegetation or soil. Rabbits do not eat the reed or the unidentified trees; the latter are the only trees that appear healthy. All trees have their roots exposed to a depth of 1–6 ft.; the pine trees are not actively growing but are setting seeds; the leaves of the *Lagunaria* are confined to the main branches so that the trees look as though recovering from a fire.

The topography of the island is steep with V-shaped erosion gullies at frequent intervals; run-off of water is extremely rapid and complete and carries extraordinary quantities of solid material. The effective rainfall is probably about 5 to 10 in. per annum overall, but the steeper parts retain practically no rain; the island was quite dry only two days after heavy rain. All soil has gone except from a few flat areas and screes, and removal of rabbits will

not now alter the island except in a very minor way.

In March 1953 myxomatosis was introduced, but further introductions were abandoned due to the difficulty of landing. It is now unlikely that any further eradication work will be attempted.

DISCUSSION

These islands provide an interesting contrast. On Phoenix Island, almost on the equator, conditions must be only just within the level of tolerance for the rabbit species, and factors other than food presumably hold the population down to a level where it does not seriously affect the vegetation. Rabbits have been on Phillip Island for nearly a hundred years and must have reached a state of equilibrium with the vegetation, most of which has been destroyed, but some plant species must survive that are both resistant to rabbit grazing and yet sufficiently palatable to support the existing rabbit population. On Lisianski Island no such equilibrium was reached, and it was thought that rabbits would similarly have gone from Laysan Island had they not been exterminated (Wetmore, 1925). Presumably the rate of increase of the rabbits quickly produced a large population, and the vegetation was destroyed to such an extent that it was unable to recover in time to maintain even a greatly reduced number of rabbits. Manana, Lehua, and Molokini islets are all subject to droughts during which the rabbit populations are drastically reduced and presumably the vegetation can recover sufficiently to survive.

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Relationships of the Red-backed Voles of Japan

E. W. JAMESON, JR.[1]

EASTERN ASIA is particularly rich in genera and species of microtine rodents, some of which are more or less intermediate between *Microtus* on the one hand and *Clethrionomys* on the other. Where species of only these two genera are concerned, there is no problem of identity because there are differences in the color, in the structure of the palate, and in the skull in general. The age of the specimen changes strikingly the condition of the cheek teeth, in which there are some of the most important generic features. Molars of immature specimens of *Clethrionomys*, for example, are rootless, and resemble in this respect the molars of adult individuals of *Microtus*. In eastern Asia there are a number of species which resemble the species of *Clethrionomys* in the palate, which terminates in a shelf, and are like *Microtus s. str.* in having rootless molars. For these forms which combine some of the structural characteristics of *Clethrionomys* and *Microtus* there are a number of generic names. A reviewer naturally wonders if his material contains mature individuals, and this doubt has caused some disagreement as to the proper generic allocation of red-backed voles of the Far East.

The red-backed voles in Japan have been discussed by Hinton (1926), whose conclusions have been accepted by Ellerman (1941) and by Ellerman and Morrison-Scott (1951). Hinton (1926: 259–262) judged that several different forms were all based on immature specimens and placed *bedfordiae*, *andersoni*, and *niigatae* as synonyms of *smithi*. He very carefully explained the pitfalls in separating voles on a small series and he emphasized the early age at which voles breed (and are apparently adult). In the Japanese forms in question, the age of the specimens is of great importance because these names were proposed for individuals in which the molars are rootless, and Hinton's conclusion was that they are all immature specimens. His caution is certainly justified but can be carried to misleading extremes, for by combining several distinct forms as one, it is not difficult to show that a given character, in this case the condition of the molar roots, is indeed remarkably variable. There are remarks in Hinton's appraisal of the situation that raise some doubts as to its application to the specimens he had at hand. For example, in reference to the small vole called *smithi*, he stated (1926: 260) that the type was a young male and added that "...by accident the fifty-three specimens of the series collected in Hondo, Kiushiu, and Shikoku, by M. P. Anderson in the following year are all young too." It is possible, of course, to sample a population and obtain a series in which immature specimens predominate; but it is incredible that such an experienced collector as Anderson would have preserved 53 specimens of *smithi* from at least three widely separated localities and fail to include a single adult. Hinton added:

> Later on Mr. Anderson collected thirteen in Hokkaido. The majority of these are adult, some even old; in size, skull form, and tooth pattern they are strikingly different from the material referred by Thomas to *E.—smithii*. These were therefore described as a new species, *E. (Craseomys) bedfordiae*. But two specimens of this original series of *E. bedfordiae* are immature, and these are not distinguishable from the material upon which *E. smithii* was founded.

These two presumably immature specimens could possibly belong to *Clethrionomys rutilus*, which is not uncommon in some parts of Hokkaido; and, in this region, *rutilus* is a small bright short-tailed form somewhat like *smithii*. On the same page he dismissed the form described as *E. (C.) andersoni* with the comment, "...specimens, however, are merely large adolescents, intermediate in age between the adult material upon which *E. bedfordiae* was established and the immature material referred to

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as *E. smithii.*" Lastly, "Anderson's *E. niigatae* also has been founded upon an adolescent animal. . . ."

Apparently Hinton attached no importance to the occurrence of immature *smithi* on Kyushu, Shikoku, and Honshu, and the absence of adult *smithi* everywhere but on Hokkaido. It is surprising that he did not consider that these forms with rootless molars might actually be adults, for on the mainland of Asia and on Taiwan are genera of red-backed voles in which the molars are rootless in the adults. Hinton recognized *Eothenomys, Anteliomys,* and *Aschizomys,* genera in which the molars are rootless; but failed to suggest any similarities between *smithi* and the species of these genera.

The classification of these voles by Japanese mammalogists differs considerably from the recent presentation of Ellerman (1941) and of Ellerman and Morrison-Scott (1951). In the latter work the authors were apparently unaware of the very careful study on Japanese murid rodents by Tokuda (1941).

In his monograph, Tokuda (1941) followed Oldfield Thomas in general in the classification of the Japanese red-backed voles. He considered *smithi* as a separate species in the genus *Clethrionomys, bedfordiae* was retained as a subspecies of *Clethrionomys rufocanus,* and *andersoni* was judged to be a distinct species but closely allied to *rufocanus.* Tokuda (1941: 51) followed Hanaoka in placing *Craseomys niigatae* as a synonym of *Clethrionomys andersoni.* Tokuda did not suggest at this time that *smithi* had affinities except in the genus *Clethrionomys.*

The first to suggest a different position for *smithi* was Imaizumi (1949), who placed it in the genus *Eothenomys.* Subsequently, Tokuda (1955) presented evidence for considering *smithi* a species of *Anteliomys.* Imaizumi (1957), considering *Anteliomys* a synonym of *Eothenomys,* continued to use the latter name, and described a second species, *Eothenomys kageus,* from the northern part of Honshu.

The most recent classification of the red-backed voles in Japan is by Imaizumi (1960). In this arrangement there are *Eothenomys: smithi* and *kageus;* and three species of *Clethrionomys: rutilus, rufocanus,* and *sikotanensis;* in contrast to Tokuda, Hinton, and other recent students, Imaizumi maintained *niigatae* as a species distinct from *andersoni,* and placed both in *Aschizomys.*

During 1952 I spent 10 months in Japan and made a small collection of voles. In 1958 and 1959 I was able to trap additional specimens of all but one (*Clethrionomys sikotanensis*) of the forms of red-backed voles in Japan, and from these specimens and the excellent discussions of Tokuda and Imaizumi, it is apparent that the original descriptions of Oldfield Thomas and the recent researches of Tokuda and Imaizumi more accurately express the relationships of these voles. The work of Hinton was executed apparently with little knowledge of the geologic history of the Japanese archipelago and without the advantage of having studied these Japanese voles in the field. The arrangement given below is, in most respects, like that accepted by Japanese mammalogists today. Because of the stature of Hinton's monograph, his conclusions have been followed by European and American zoologists, and reiterated, in regard to the rodents in question, by Ellerman (1941) and Ellerman and Morrison-Scott (1951). The environmental distributions and economic importance of these voles is discussed by Ota and Jameson (in press).

GENUS *Clethrionomys* Tilesius

Originally all the red-backed voles in Japan were placed in *Clethrionomys.* The Japanese *C. rutilus mikado* exists only on the island of Hokkaido. In general appearance and in most details *rutilus* closely resembles the other species of *Clethrionomys s. str.* The skull is light with rounded contours, the palate is abnormal (differing from *Microtus*), the cheek teeth are relatively light and are rooted in the adult. The mammae are in four pairs. The species in this genus are characterized by other features but the above are sufficient to separate *rutilus* from the other species of microtine rodents in Japan.

The species *rufocanus* has long been known as a rather aberrant species of *Clethrionomys.* Miller (1898*a*: 360) treated in some detail the distinctive characters of this vole:

So divergent is the animal that it may well be questioned whether it is to be regarded as a true

Evotomys (= *Clethrionomys*). Its heavy and apparently imperfectly rooted teeth more closely resemble those of many species of typical *Microtus* than they do the weak, perfectly rooted teeth of true *Evotomys*. The relationship of the root of the lower incisor and the posterior lower molar, while not typical of either genus are clearly suggestive of *Microtus* rather than *Evotomys*. The palate structure, on the other hand, appears to agree with that of *Evotomys*.

Also, in a key to the Arctic species of red-backed voles Miller (1898*a*: 359) separated *rufocanus* by the comment: "Teeth large and heavy as in *Microtus* (never perfectly rooted?)...." In characterizing *rufocanus*, Hinton (1926: 245) also emphasized its approach to the species of *Microtus* and on page 215 pointed out that individuals look mature "long before the molars show the slightest sign of rooting." To distinguish *rufocanus* from the other species of *Clethrionomys* Miller (1900) created the subgenus *Craseomys* with the following characters:

Skull as strongly angular as in *Microtus*, the postorbital processes well developed; teeth relatively as large as in *Microtus*, the molar row about equal to the diastema; roots of molars developed late in life; root of posterior lower molar lying in a distinct capsule on the lingual side of incisor root.

Soon after Thomas (1905) placed the Japanese forms *bedfordiae* and *andersoni* in the subgenus *Craseomys*. Later (1907), he used *Craseomys* as a genus for *Craseomys regulus* (=*Clethrionomys rufocanus regulus*) from Korea and noted that not even the oldest in the series of 18 specimens showed any trace of roots on the molars.

Aschizomys lemminus was described as a new genus and species by Miller (1898*b*) on the basis of a single specimen and was characterized in these terms: "Palate as in *Clethrionomys*. Molars small and weak, as in *Clethrionomys*, but teeth growing from a persistent pulp as in *Microtus*) which strongly displaces root of large posterior lower molar. Plantar tubercles six. Number of mammae unknown." The illustrations accompanying the original description indicate other features common to both *lemminus* and *rufocanus:* the encapsulated roots of the upper second molar and the lower third molar and the reduced lateral tubercles on the rostrum. The upper third molar of *lemminus* is longer than in *rufocanus* and there is little doubt that the two species are separate. The third upper molar of *Clethrionomys niigatae* of northern Honshu is long and similar to *lemminus*. In the original description of *Aschizomys* Miller recommended that *rufocanus* was allied to *lemminus* and later Imaizumi (1957: 199) suggested that *Clethrionomys niigatae* might well be placed in *Aschizomys*. Also, Hinton (1926: 43) stated that *lemminus* seemed to be very close to *rufocanus*. However, as Miller suggested (1898*a*: 359), the molars of *rufocanus* form roots very late in life; it is quite possible that *rufocanus* and *lemminus* are alike in this respect as well, and that a large series of *Aschizomys lemminus* would probably contain a few individuals old enough to have partly rooted molars. Granting this supposition, a reasonable arrangement would be to place *rufocanus* with *lemminus* in *Aschizomys*.

In this case *Craseomys* Miller, 1900 will become a synonym of *Aschizomys* Miller 1898. Recent authors have regarded *Craseomys* a synonym of *Clethrionomys;* perhaps because they considered it unnecessary to retain a subgenus which contained but a single species. In placing *rufocanus, niigatae, andersoni,* and a new species from Honshu together with *lemminus* all in *Aschizomys*, one must decide the proper position of this group. Although Miller preferred to call it a genus, he did consider that *Aschizomys* could be placed with *Eothenomys* and *Anteliomys*. *Eothenomys* combines characters of *Microtus* and *Clethrionomys;* and *Aschizomys* (including *rufocanus* and *andersoni*) bridges the gap between *Eothenomys* and *Clethrionomys*.

As pointed out by Ellerman and Morrison-Scott (1951: 670), Russian authors place *Aschizomys* as a subgenus of *Alticola*. The two groups are certainly very close; but, if I am correct in presuming that very old specimens of *Aschizomys lemminus* will tend to develop roots on the molars, then *Aschizomys* is more appropriately placed with *Clethrionomys*.

Inasmuch as a few old individuals of *rufocanus* and *niigatae* have partly rooted molars, it seems best to place *Aschizomys* as a subgenus under *Clethrionomys*, and the forms known in Japan can be separated by the key below.

KEY TO SPECIES OF *Clethrionomys* IN JAPAN

1. Molars developing long roots in adults; postorbital crests poorly developed or absent; second upper molar and third lower molar not encapsulated in adults: (subgenus *Clethrionomys*) ..... *rutilus*

   Molars rootless except in very old adults; postorbital crests well developed; second upper molar and third lower molar usually encapsulated in adults (subgenus *Aschizomys*) 2

2. Third upper molar with three inner salient angles (Fig. 1); tail less than one-half the body length; on Hokkaido ..... *rufocanus bedfordiae*

   Third upper molar with more than three inner salient angles or loops although some projections may be irregular or rounded (Fig. 1); on Honshu 3

3. Salient angles of all cheek teeth rounded or irregular, and triangles often open (Fig. 1); auditory bullae relatively small; in low elevation evergreen broad leaved forests of extreme southern Honshu ..... *imaizumii*

   Salient angles more or less pointed, and triangles usually closed; auditory bullae relatively large; in coniferous forests of the northern half of Honshu 4

4. Rostrum relatively long; anterior palatine foramina arise from about level of anterior molar alveolae; upper molar tooth row more than 6.0 mm ..... *niigatae*

   Rostrum shorter; anterior palatine foramina arise from a point distinctly anterior to the level of anterior molar alveolae; upper molar row less than 6.0 mm ..... *andersoni*

Clethrionomys rufocanus bedfordiae (Thomas, 1905)

Evotomys bedfordiae Thomas, 1905, Abstracts, Proceedings, Zoological Society of London, no. 23. (Holotype from Shinshinotsu, near Sapporo, Hokkaido.)

This is the form of *rufocanus* which occurs on the northern island, Hokkaido. It is a large, richly colored species with a tail of moderate length. It is difficult to compare *bedfordiae* with the other named subspecies: the illustrations of *rufocanus shanseius* (of the adjacent mainland) in Hinton (1926) are made from specimens which perhaps are not *rufocanus* and may not even belong in *Clethrionomys*. Presumably the nearest relatives live on the island of Sakhalin and the adjacent mainland. *Clethrionomys sikotanensis* (Tokuda, 1935) seems to be quite distinct from, although allied to, *rufocanus; sikotanensis* is known from the Southern Kuriles and may be more closely related to *lemminus*.

The skull of *bedfordiae* resembles the illustration of *C. r. rufocanus* in Hinton (1926: fig. 80); the depicted specimen is from an unspecified locality. Hinton's illustration of *C. r. shanseius* (1926: fig. 83) is from the type series of *Caromys inez; shanseius* (from China) should be closer to *bedfordiae* than is typical *rufocanus* (from Sweden), but there is little doubt that Hinton's illustration of *shanseius* represents a form at least specifically distinct from *rufocanus*. The enamel pattern (Fig. 1) is typical of *C. r. bedfordiae* and the third upper molar is especially characteristic. In 22 adults examined, 2 have distinctly rooted molars; in 8, the pulp cavities are more or less closed off, indicating that roots would probably have formed later in life. The anterior palatine foramina are expanded anteriorly and quite narrow posteriorly and resemble *C. r. rufocanus* in this respect. The tail is less than one-half the body length.

C. rufocanus bedfordiae is the most abundant microtine mouse on Hokkaido and is almost always more common than *C. rutilus*. In the absence of any competing species of *Microtus* (which does not occur on Hokkaido), *rufocanus* is sometimes a common inhabitant of open meadows and is of considerable economic importance (Ota and Jameson, in press).

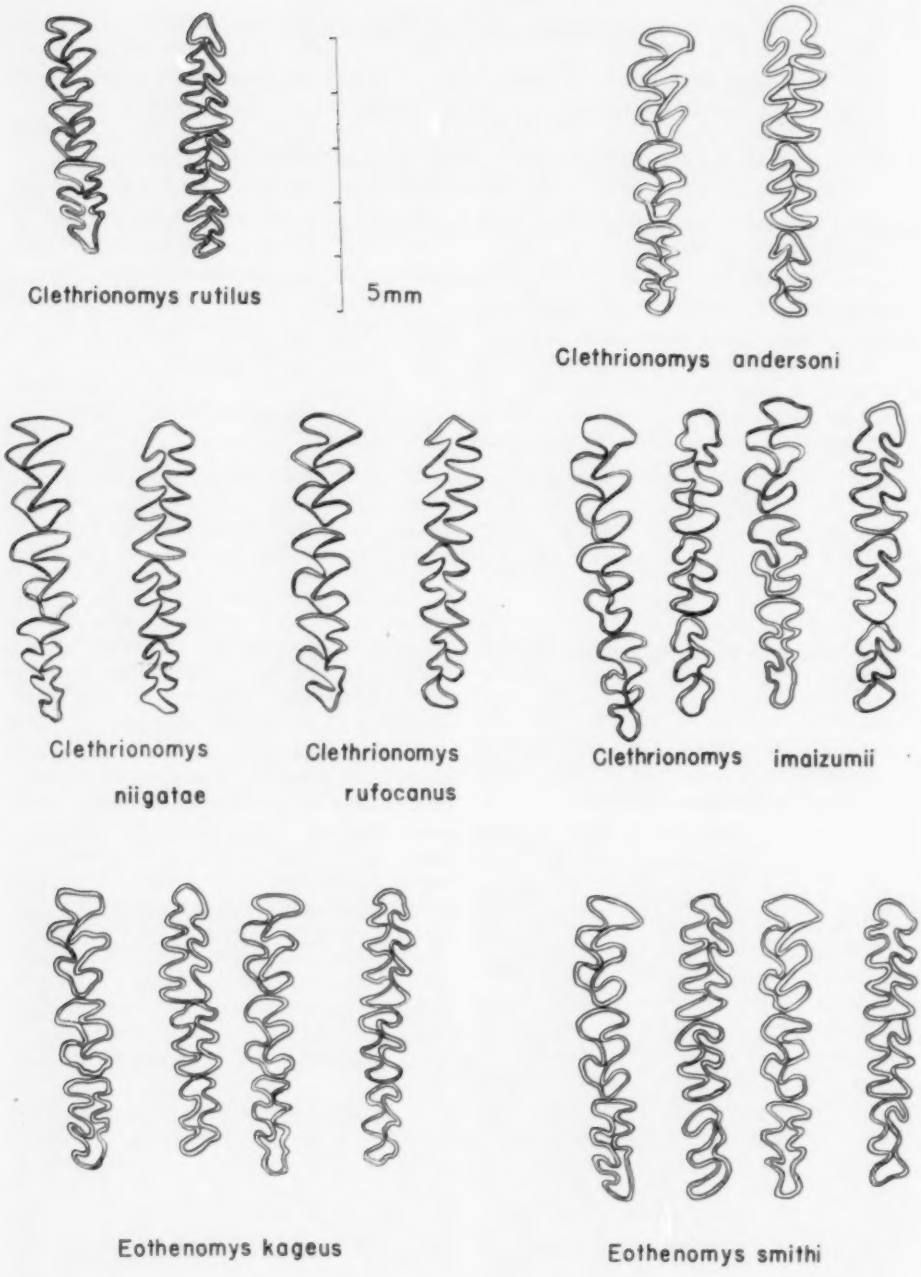

FIG. 1. Enamel patterns of Japanese red-backed voles.

Clethrionomys andersoni (Thomas, 1905)

Evotomys andersoni Thomas, 1905, Abstracts, Proceedings, Zoological Society of London, no. 28. (Holotype, from Tsunagi, Iwate-ken, Honshu.)

This form is sometimes considered to be a subspecies of *rufocanus,* to which it is closely related. *C. andersoni* is easily separable from *C. rufocanus bedfordiae* by the longer third upper molar, which has four inner salient angles. *C. andersoni* is close also to *C. niigatae,* which is sometimes considered to be the same. Examination of specimens of the type series of both *andersoni* and *niigatae* indicated that the two are distinct and that adults can be identified by the above key.

C. andersoni is an inhabitant of coniferous forests in northern Honshu, in Aomori-ken, Fukushima-ken, and Iwate-ken, according to Imaizumi (1960: 134).

Clethrionomys niigatae (Anderson, 1909)

Craseomys niigatae Anderson, 1909, The Annals and Magazine of Natural History, vol. 4, ser. 8: 317. (Holotype from Akakura, Niigata-ken, Honshu.)

For a very long period *C. niigatae* had been considered to be a synonym of *C. andersoni;* but, after studying specimens from the type series of both species, I agree with Imaizumi (1960) that the two are distinct species. In the nine adults examined, one specimen has closed pulp cavities and incipient roots. This is in contrast to the specimens examined by Imaizumi (1957 and 1960); the series in the National Science Museum in Tokyo all possess rootless molars. *C. niigatae* lives in the higher elevations of central Honshu. In Nagano-ken, it is found at approximately 1900 m. and higher among boulders both in virgin forests of fir and spruce and in rather open tangles of wild raspberries and currants.

Clethrionomys imaizumii, new species

TYPE: Adult male, skin and skull. Collected 13 Feb. 1959, Nachi Falls, 300 feet elevation, Wakayama-ken, Honshu, Japan; E. W. Jameson, Jr., no. 1083.

RANGE: Probably in broadleaved forests at low elevations in extreme southern Wakayama-ken (Kii Peninsula).

DIAGNOSIS: A rather large, brightly colored, long-tailed species of the subgenus *Aschizomys.* Dorsum Rood's Brown; venter Sayal Brown; tail bicolor, thinly haired, as in *rufocanus* and *andersoni* (color from Ridgway, 1912). Skull with rather small auditory bullae. Molars with angles rounded.

MEASUREMENTS (in mm.): Holotype (and paratype): Total length, 194 (184); tail, 67 (61); hind foot, 22 (21). Skull: condylobasilar length, 29.1 (skull of paratype damaged); zygomatic breadth, 15.6 (15.1); interorbital breadth, 4.3 (4.4); lambdoidal breadth 12.5 (—); alveolar length of upper molar row, 6.9 (6.3); diastema, 8.3 (7.7).

This species is most nearly like *C. niigatae,* but differs strikingly in the color and dentition. The molars are rootless with open dentine spaces in the two adult males seen. The enamel pattern is quite different, however: the triangles are rounded and indistinct and frequently open (Fig. 1). The auditory bullae are markedly smaller.

This species inhabits the luxuriant hardwood forests of the southern part of the Kii Peninsula in Wakayama-ken, the southernmost part of Honshu. Specimens were first collected by Dr. R. Kano; and Dr. Yoshinori Imaizumi kindly directed me to collecting localities.

These four forms of the subgenus *Aschizomys* are separable on external characters, and these features are substantiated by constant dental and other cranial morphology. The relative proportions of the tail and body lengths are rather different for *rufocanus,* on the one hand, and for *andersoni, niigatae,* and *imaizumii* on the other hand. *C. niigatae* and *C. imaizumii* are long tailed. In nine specimens of *niigatae* from the upper slopes of Yatsugatake, the tail is from 58 to 66 mm. in actual length, and the tail length is from 51 to 62 per cent of the body length. In a series of 22 adults of *C. rufocanus bedfordiae* from various localities in Hokkaido, the tail is from 34 to 56 mm., and the tail length is from 28 to 46 per cent of the body length. It is quite possible that large series of both species would show some

overlap in this character but the difference is nevertheless real and fairly constant. *C. imaizumii* is a long-tailed animal like *niigatae*. The general fascies of the enamel patterns of *C. rufocanus bedfordiae*, *C. niigatae*, and *C. andersoni* are angular (Fig. 1), but *andersoni* and *niigatae* are distinct in having four inner salient angles in the third upper molar, whereas *rufocanus bedfordiae* has three. The enamel pattern of *imaizumii* is quite different in having the angles rounded, and there is a tendency for the loops and triangles to remain open (Fig. 1). The four species differ also in the form of the anterior palatine foramina. The hind foot of *rufocanus bedfordiae* is more densely furred than that of *niigatae*, *imaizumii*, and *andersoni*, but all species are alike in possessing six plantar tubercles between which there are tiny projections.

Imaizumi (1957) intimated that *niigatae* might be generically distinct from *rufocanus bedfordiae* because the molars are rarely rooted in *bedfordiae* and seemed never to be rooted in *niigatae*. In one specimen of *niigatae* examined by me, the pulp cavities are closed and there are incipient roots. Later (1960) Imaizumi placed *niigatae* and *andersoni* in *Aschizomys* and kept *rufocanus* in *Clethrionomys*; but such an arrangement does not indicate the nearness of these three species. As will be pointed out later in this paper, *andersoni* and *niigatae* almost certainly emigrated from Hokkaido from a stock close to *rufocanus*. Imaizumi's suggestion, reasonable as it may seem, simply emphasizes the weakness of the presence or absence of molar roots as a generic character in this case.

Clethrionomys rutilus mikado (Thomas, 1905)

Evotomys mikado Thomas, 1905, Abstract, Proceedings, Zoological Society of London, no. 23, p. 19. (Holotype from Aoyama, Hokkaido.)

This bright red little vole is quite unlike any other species in Japan. The color, rounded enamel pattern (Fig. 1), well-developed molar roots, and small size separate *rutilus* from *rufocanus*, the only other vole in Hokkaido. The molar row is rather short, as in *Eothenomys smithi* and *E. kageus*, and the enamel patterns are similar, but the angles are less rounded. In *C. rutilus* there are four pairs of mammae. One specimen was examined.

C. rutilus mikado is a rather uncommon dweller of the forests of Hokkaido and is not known to occur elsewhere in Japan.

GENUS *Eothenomys* Miller

The other genus of red-backed voles in Japan is *Eothenomys*; most of the species occur in China and one (*melanogaster*, the type of the genus) is found also on Taiwan. These species are quite close to *Clethrionomys* in general and some of them are perhaps related to the species of the subgenus *Aschizomys* in particular. In *Eothenomys* the color is highly variable, but some species are reddish and so resemble the species of *Clethrionomys*, with which they have been confused on more than one occasion. *Eothenomys* differs in possessing rootless molars and only two or three pairs of mammae. Even in the oldest specimens there is no closure of the pulp cavities. The skull of *Eothenomys* is light and delicate and tends to be rounded; and the palate terminates in a shelf, as in *Clethrionomys*.

KEY TO SPECIES OF *Eothenomys* IN JAPAN

1. Mammae four ..... *kageus*
   Mammae six ..... *smithi*

Eothenomys smithi (Thomas, 1905)

Evotomys smithi Thomas, 1905, Annals and Magazine of Natural History, series 7, vol. 15, p. 493. (Holotype from Kobe, Honshu.)

In Japan, the species *smithi* was described from specimens from Kobe, on the island of Honshu; *smithi* is also a common species on Shikoku and Kyushu, and a shorter-tailed subspecies (*okiensis*) was described from the island of Dogo in the Oki Group. The species *smithi* was described by Thomas in 1905, who at that time placed it in *Evotomys* (= *Clethrionomys*); and, noting some differences from the morphology of most species of that genus, he erected the subgenus *Phaulomys*. Thomas stated then that *smithi* showed characters of *Evotomys*, *Eothenomys*, and *Anteliomys*. Externally *smithi* is similar to species of *Clethrionomys*, except that there are two or three pairs of mammae

instead of four pairs. The form of the skull resembles that of *C. rutilus* and the other species of *Clethrionomys s. str.* (not including *rufocanus, andersoni, imaizumii,* and *niigatae*): the skull is delicate and rounded and the postorbital projections are barely developed. The enamel pattern tends to be rounded rather than angular; Thomas noted that the closed triangles tend to be little broader than long (Fig. 1). *Phaulomys* stands apart from *Clethrionomys* because the molars are rootless in the adult. Thomas also pointed out the encapsulated root of the second upper molar which projects into the orbital fossa; this invariably occurs in microtine rodents when the molars are not rooted and is simply another way of stating this condition. Since the description of *smithi,* many hundred of specimens have been collected and the molars are known to be rootless even in old adults. (Hinton's [1926] observation to the contrary resulted from his confusing *Clethrionomys rufocanus bedfordiae* and perhaps *C. rutilus mikado* with *smithi.*) Recent studies by Japanese workers (e.g., Tokuda, 1955, and Imaizumi, 1957) indicated that *smithi* is allied to the Chinese species of *Anteliomys* (a synonym or subgenus of *Eothenomys*), and the proper name for this species is *Eothenomys smithi.* Nineteen specimens were examined.

Eothenomys kageus Imaizumi, 1957

Eothenomys kageus Imaizumi, 1957, Bulletin, National Science Museum (Tokyo), vol. 3, no. 3, p. 204. (Holotype from Yamuramachi, Minamitsuru-gun, Yamanashi-ken, Honshu.)

Imaizumi (1957) named the form from the northeastern part of Honshu as *E. kageus.* From the detailed description of *kageus,* it is apparent that *kageus* and *smithi* are very close. *E. kageus* has two pairs of mammae whereas in *smithi* there are three pairs. The size, color, and body measurements of *E. kageus* are very close to those of *E. smithi.* The enamel patterns of the two species are also very similar (Fig. 1). The original description of *E. kageus* included a difference in the posterior angle of the zygomatic arch; but the explanatory drawing (Imaizumi, 1957: fig. 3) indicated that the angle measured on *E. kageus* was different from that taken from *E. smithi,* and the data are not comparable. The differences in the bacula of *E. kageus* and *E. smithi* may be due to individual variation: specimens of both species are extremely variable and there seem to be no constant differences in the bacula of the two named forms (Fig. 2). Six specimens were examined. Future studies may reveal that *E. kageus* is a subspecies of *E. smithi.*

Eothenomys smithi and *E. kageus* are similar in habits and habitat. They dwell in forested regions from sea level to elevations of 2500 m. or more, but generally do not occur together with *Clethrionomys niigatae, imaizumii,* or *andersoni.* On Yatsugatake, *E. kageus* occurs up to about 2000 m., above which level *C. niigatae* is found; but on the eastern slope of Ontake, where *C. niigatae* does not occur, *E. smithi* extends well above 2000 m. (Tokuda, 1950); and on Mt. Fuji (where *C. niigatae* is absent) *E. kageus* is found to the upper limit of the forest (Imaizumi, 1944). On Kyushu, *E. smithi* is the only red-backed vole, and it lives in wooded areas from at or near sea level to the highest peaks, becoming more abundant at the higher elevations. On Shikoku, where *Microtus montebelloi* is not found, *E. smithi* may move from the forest to relatively open grassy or brushy areas (Ota and Jameson, in press). *Eothenomys* does not occur on Hokkaido.

The bacula of the red-backed voles in Japan (Fig. 2) are rather variable within a given species, and provide rather poor taxonomic characters at the specific level. Some of the smaller bacula are obviously from young animals but even examples of the same size may be remarkably dissimilar. There are differences in both size and shape of the shaft and its base as well as in the three prongs. There seem to be no distinctions between the bacula of *Eothenomys kageus* and *E. smithi* unless the shaft in *kageus* is slightly more slender. There are probably no differences between the bacula of *Clethrionomys niigatae* and *C. rufocanus bedfordiae,* but *C. imaizumii* has relatively larger prongs which are rather divergent, and in this respect resembles those of some species of *Microtus.* Most bacula of these voles have a slight keel on the median tyne, a character of the bacula of both *Clethrionomys* and *Microtus.* No bacula of *C. andersoni* were available.

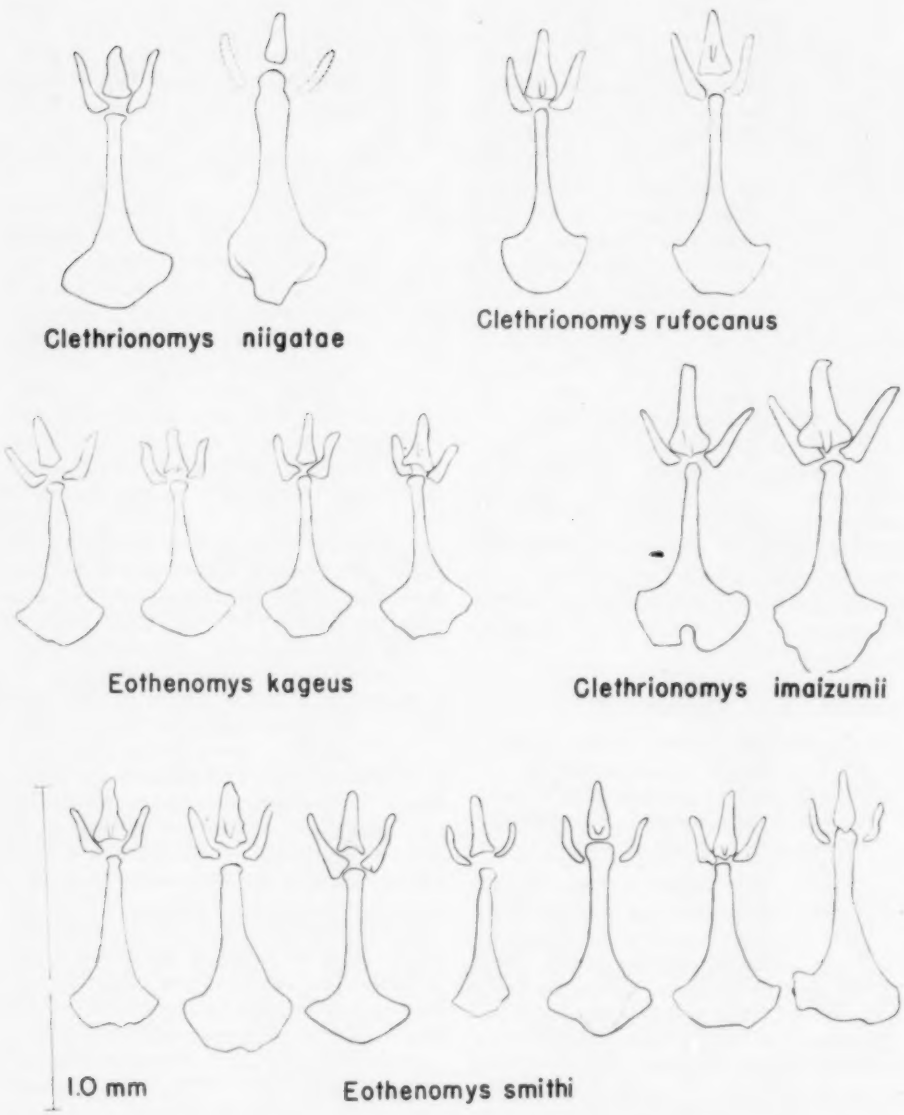

FIG. 2. Bacula of Japanese species of *Eothenomys* and *Clethrionomys* (*Aschizomys*).

GEOGRAPHIC ORIGIN OF RED-BACKED VOLES IN JAPAN

In the Pleistocene and earlier the present archipelago of Japan was connected to the mainland in the south, between Kyushu and the Korean Peninsula, and in the north, between Hokkaido, Sakhalin, and adjacent Siberia. At approximately the same time, changes resulted in the separation of Kyushu and Korea, and also the formation of the Tsugaru Strait between Hokkaido and Honshu. Consequently, the islands of Kyushu, Shikoku, and Honshu no longer received immigrants from the continent, and they were isolated from the effects of faunal movements on the mainland. Today, the fauna of the old islands of Kyushu, Shikoku, and Honshu is, in many respects, quite different from that of the immediately adjacent mainland, and has its closest affinities to the southwest in China. This faunal difference has been mentioned as early as Thomas' 1905 paper. On the other hand, Hokkaido and Sakhalin remained part of the mainland and were subjected to the faunal changes that affected southeastern Siberia and Korea. There are no land mammals in Hokkaido that are more than subspecifically distinct from those of nearby Siberia and Korea. The important and extensive movements of mammals in this general area during the Pleistocene (see Simpson, 1947: 643) changed the fauna of Hokkaido, replacing with more recent forms the original fauna that now remains in the older Japanese islands.

Eothenomys smithi probably entered Japan on the old route between Korea and Kyushu via a connection which remains today as the islands of Tsushima and Iki. *E. smithi* moved on from Kyushu to Shikoku and is now the only microtine rodent known from the latter island. This vole moved also to Honshu and now occupies a large part of that island, at least to southern Nagano-ken. *E. smithi*, or its progenitor, at one time must have occurred in Korea although the genus is not there now. *E. kageus* may have come from the north via Sakhalin and Hokkaido, although its occurrence is now confined to the northern half of Honshū south to where it abuts the geographic range of *E. smithi*. The changes which resulted in the extinction or the emigration of *Eothenomys* from Korea and Siberia apparently affected Hokkaido as well. Actually, it seems likely that *E. smithi* and *E. kageus* are offshoots from a single ancestor which differentiated slightly along the coast from Korea to Siberia so that different subspecies entered Kyushu and Hokkaido. This could account for the great similarity between these two forms that now occupy adjacent but not overlapping geographic areas.

Similarly, the species of *Clethrionomys* came to Japan by two routes. *C. imaizumii*, which is now known only from the low elevations of Wakayama-ken, may have its relatives among one of the many kinds of red-backed voles described from China. This is conjecture, but this vole is now associated with a semitropical flora of broad-leaved hardwoods. This species, moreover, is morphologically quite distinct from *C. andersoni*, *C. niigatae*, and *C. rufocanus bedfordiae*, which are found in forests of fir (*Abies* spp.) and spruce (*Picea* spp.). *C. niigatae* and *C. andersoni* are almost certainly arrivals via Hokkaido. Although *niigatae* and *andersoni* are close relatives of *C. rufocanus bedfordiae*, they may have been derived from an earlier stock. Hokkaido and Honshu were separated since before the Pleistocene, and *niigatae* and *andersoni* were immune to the immigrants of *C. rufocanus bedfordiae*. Not only are the three species close morphologically, but they share three species of fleas which are parasites of *C. rufocanus* in Hokkaido: *Catallagia striata*, *Megabothris sokolovi*, and *Rhadinopsylla alphabetica*. One (*Catallagia striata*) occurs also in Siberia and another (*Megabothris sokolovi*) in the Kuriles.

The occurrence of *C. rutilus* needs little explanation. It is obviously a rather recent arrival in Hokkaido. If it ever extended to Honshu, it did not persist, and it may well have entered Japan after the separation of Hokkaido from Honshu.

SUMMARY

There are seven species of red-backed voles in Japan. *Clethrionomys* (*Clethrionomys*) *rutilus* occurs in Hokkaido. The species *andersoni*, *niigatae*, and *imaizumii* (from Honshu) and *rufocanus* (from Hokkaido) are considered to represent *Aschizomys*, which is placed as a subgenus of *Clethrionomys*. *Eothenomys smithi* in-

habits Kyushu, Shikoku, and Honshu, and *E. kageus* occupies the northern half of Honshu.

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Two Shark Incidents at Eniwetok Atoll, Marshall Islands[1]

E. S. HOBSON,[2] F. MAUTIN,[3] and E. S. REESE[2]

THE TWO SHARK INCIDENTS described in this paper can be be considered as unprovoked shark attacks (Gilbert *et al.* 1960: 324). The importance of documenting these incidents is that they were observed by persons with some experience in the study of animal behavior. The great need of precise and detailed observational information on shark attacks has been stressed in recent reports on the subject (Coppleson, 1958: ix; Gilbert *et al.*, 1960: 323; Tester, 1960: 181). It is the belief of the authors that well-documented reports of shark incidents will contribute significantly to a clearer understanding of the stimulus situations in which shark attacks on man can be expected.

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FIRST INCIDENT

At noon on September 1, 1960, Hobson, Mautin, and Reese were engaged in spear fishing activities on a reef about 25 ft. below the surface and approximately 200 yd. from shore on the lagoon side of Parry Island, Eniwetok Atoll, Marshall Islands. Dr. Richard A. Boolootian of the University of California was in a 16-ft. skiff powered by a 35-hp. outboard motor which was idling nearby. The sea was calm, there was very little wind, and the sky was clear. Underwater visibility was in excess of 100 ft. Table 1 indicates the nature of the equipment that was being used. The spatial relationship of the divers to one another and to the skiff above the reef at the start and the end of the encounter is shown in Figure 1.

Hobson speared a 25-lb. grouper (*Plectropomus* sp.), which swam, trailing the spear, beneath a large coral boulder (rock 1, Fig. 1). Almost immediately three grey sharks (*Carcharhinus menisorrah*, Fig. 2), approximately 5–7 ft. in length, appeared from the deep water of the lagoon and began to circle the rock. Hobson observed (1) the sharks were swimming in an excited manner, and (2) they paid no attention to him floating quietly on the surface. Suddenly the grouper broke cover and dashed to a second large coral boulder (rock 2, Fig. 1). The three sharks immediately followed and began to circle the second rock.

Reese, who was directly above rock 2, noticed the sharks and was also impressed with the excited appearance of their swimming. Meanwhile, Hobson swam towards rock 2 to inform Mautin and Reese of the speared fish and the excited sharks in the area. At about this time Mautin observed the sharks and noted their excited state. All three began to swim toward the skiff, making a conscious effort not to produce an undue amount of commotion on the surface. There were now four or five sharks swimming in an excited manner on the reef below. Mautin, who was unarmed and farthest from the boat, was swimming strongly in an effort to join the others. Both Hobson and Reese observed that Mautin's swim-fins were breaking the surface of the water resulting in clouds of bubbles being carried beneath the surface at each down stroke.

The following sequence of events was very rapid. Almost simultaneously with the above observation, Mautin had reached a position almost above rock 2 (see Fig. 1). Suddenly one of the sharks rose from the bottom and swam very fast in a direct line towards Mautin. Mautin saw the approaching shark and rolled on his right side

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TABLE 1

PHYSICAL CHARACTERISTICS OF DIVERS AND NATURE OF EQUIPMENT USED AT TIME OF FIRST INCIDENT

	HOBSON[1]	MAUTIN	REESE
Weight	180	195	175
Height	5′ 10″	6′ 3″	5′ 9″
Skin color	brown	brown	brown
Bathing suit	khaki	none	gray & white
Swim fins	light blue	yellow	black
Mask	dark blue	white	dark blue
Snorkel	green	white	black
Spear	Hawaiian sling with 6-ft. free shaft	none	Hawaiian sling with 6-ft. free shaft

[1] Same equipment in second incident.

in order to face the onrushing shark. When the shark was very close he kicked it violently on the snout with his swim-fins. The shark veered away, circled once or twice behind Mautin and, upon the approach of Hobson and Reese, swam away. All three swimmers were now quiet in the water.

Immediately after the first shark left the bottom, a second shark began to swim toward the surface on the same course as the first shark. However, after approaching approximately halfway, it returned to the reef floor. It is suggested that the cessation of commotion on the surface

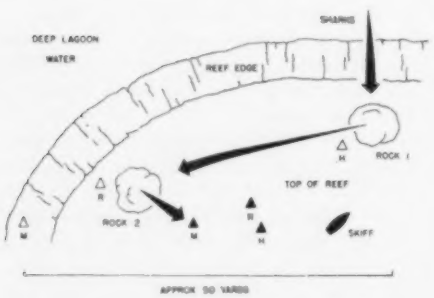

FIG. 1. Spatial relationship of divers to one another and to skiff above the coral reef at start of incident (white triangles) and at time of shark attack (black triangles). Letters beside triangles refer to diver which they represent, H = Hobson, M = Mautin, and R = Reese. Arrows indicate direction of movement of sharks.

and the presence of three swimmers resulted in the first shark swimming away and the second shark returning to the bottom.

Both Hobson and Reese were approximately 20–30 ft. from Mautin at the time the first shark attacked; however, there was no indication that the shark directed any attention toward them. It appeared that the shark was orienting to the agitation at the water's surface caused by Mautin's strong swimming. This observation supports the suggestion by Tester (1960: 183) and others that sharks are attracted by unusual commotion. A second possibility is that the shark was attracted to the bright yellow swim-fins which Mautin was wearing, but Hobson, on the basis of unpublished data, feels that this is unlikely.

Mautin gained the impression that the shark came for him believing he was the wounded fish, and that competition from the other sharks resulted in the direct and swift attack not prefaced by the usual cautious investigation.

The four to five sharks were still swimming in the same excited manner in the vicinity of rock 2 when the divers left the water.

SECOND INCIDENT

A second incident occurred the following day, September 2. Again the time was approximately noon, the sky was clear, and the surface of the lagoon was calm with underwater visibility in excess of 100 ft. Fish were being speared in shallow water along the beach at Sand Island adjacent to the deep water channel leading into the lagoon from the east. Hobson was in the water, and John C. Kay, a graduate student at the University of Hawaii, was standing off the beach in a 16-ft. skiff with the outboard motor idling. Hobson speared a 10-lb. parrot fish (Scaridae) which carried the spear shaft toward deeper water. About 35 yd. from the beach, at the edge of the reef, the bottom drops abruptly from approximately 15 ft. to over 100 ft. Grey sharks are common along this drop off. Hobson pursued the fish along the bottom, thus avoiding the surface commotion which had apparently attracted the attention of the sharks the day before. He overtook the injured fish on the bottom at a depth of approximately 15 ft. on the edge of the drop off. When the trailing spear

shaft was grasped, the fish struggled free. At the same instant a 6-ft. grey shark (*Carcharhinus menisorrah*) was upon Hobson, swimming at a slightly upward inclination directly at his face. The mouth of the shark was open, and movement of the jaws was distinctly recalled. Instinctively Hobson projected his right arm, catching the onrushing shark under the head. This, combined with a twisting, ducking motion, diverted the shark's forward rush over Hobson's left shoulder. The shark turned abruptly and circled so close that the spear which was still in the left hand could not be brought into play. As the shark circled, Hobson turned with it, pushing it away several times with his open hand until the shark was circling at a distance of approximately 4 ft.—enough room to bring the spear into use. The blunt end, which happened to be the end toward the shark, was used as a prod, and after a few jabs the shark opened its circle to approximately 10 ft. The shark appeared to be rapidly losing its aggressiveness. It seemed that apprehension toward the diver was now displacing the attack response which had asserted itself seconds before. As the boat approached, the shark fled into the adjacent deep water. The entire incident lasted only a few seconds and took place entirely on the bottom.

The shark was recognized by a deformation of the dorsal fin as one which had been involved in many of the behavior experiments conducted during the summer. It was, therefore, very familiar with the sight of humans in the water. There had been no apparent hesitation involved in its attack. Presumably its approach was made from deep water, coming over the edge of the reef which was within 10 ft. of the attack site. An approach from any other direction would have been observed.

Although the use of bare hands in warding off a shark has generally been discouraged (Gilbert *et al.*, 1960: 326), this was the only recourse in the present situation. The effectiveness of the hands in this case was no doubt largely due to the relatively small size of the shark. No lacerations of the hands occurred.

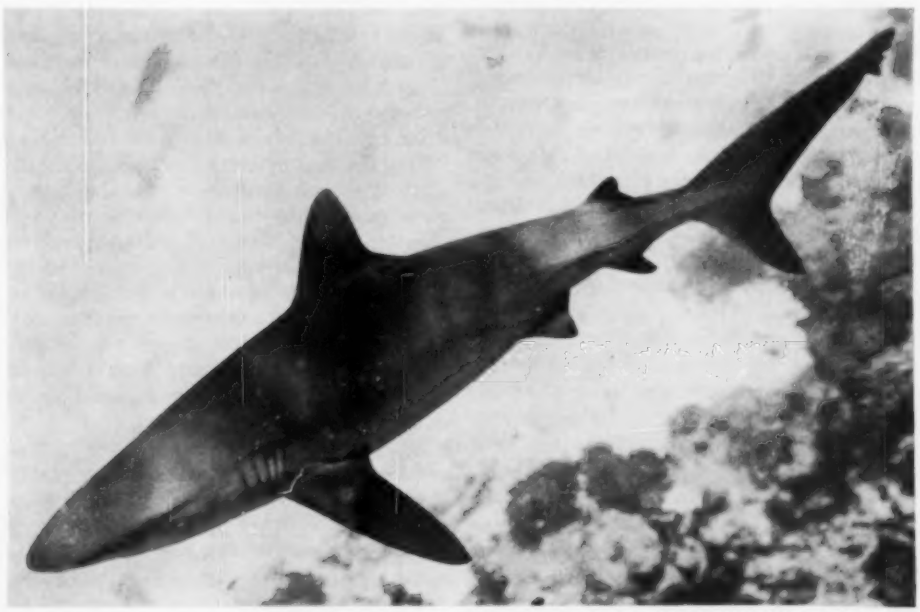

FIG. 2. *Carcharhinus menisorrah*, the species which was involved in both incidents, is common in the lagoons of most Pacific atolls, attaining a length of about 7 ft. (Photo: E. Hobson.)

TABLE 2

SUMMARY OF SIMILARITIES AND DIFFERENCES BETWEEN THE TWO INCIDENTS

	FIRST INCIDENT	SECOND INCIDENT
Activities at time of incident	spear fishing	spear fishing
Dead or injured fish present	yes: 1	yes: 1
Skin diving or SCUBA	skin diving	skin diving
Species of shark	*Carcharhinus menisorrah*	*Carcharhinus menisorrah*
Number of sharks in area	3–5	1
Size of sharks (length)	5–7 ft.	6 ft.
Date	Sep. 1, 1960	Sep. 2, 1960
Time of day	approx. noon	approx. noon
Condition of sky	clear, few clouds	clear, few clouds
Condition of sea	calm	calm
Location of incident	lagoon, Eniwetok	lagoon, Eniwetok
Distance from shore	200 yd.	35 yd.
Near deep water	yes	yes
Underwater visibility	100 ft. +	100 ft. +
Depth of water	25 ft.	15 ft.
Depth at which incident occurred	surface	15 ft., bottom
Water temperature	approx. 85° F.	approx. 85° F.
Nature of bottom	coral reef	coral reef
Number of persons in water	3	1
Nature of approach	direct, fast	direct, fast
Area of body approached	feet	head
Persistency of shark	moderate	considerable

DISCUSSION

The two incidents are summarized in Table 2. The authors believe that neither the coloration of the swimmer's equipment, the condition of the water, nor the time and nature of the day are significant. There are four major differences between the two incidents which are believed to be significant: (1) the number and relative positions of persons in the water, (2) the number of sharks in the vicinity, (3) the site of the incidents, the first on the surface, the second on the bottom, and (4) the location of the diver relative to the wounded fish. There are three major similarities between the two incidents which are believed to be significant: (1) both occurred in the vicinity of, and subsequent to, the spearing of a fish; (2) both occurred near deep water; and (3) both involved the same species of shark, which attacked without hesitation.

The last point may be explained by two facts. First, throughout the summer, Hobson, Mautin, and others noticed that *C. menisorrah* was a far more aggressive shark than the other two species which are common in the lagoon (*C. melanopterus* and *Triaenodon obesus*). This view is supported by Harry (1953: 48), who reports that the natives of the Tuamotus fear this species and claim it will attack man. Second, both incidents occurred within approximately a mile of where shark behavior experiments were conducted throughout the summer. Hobson recognized the shark in the second incident as having been a participant in these experiments, and it is probable that the sharks involved in the first incident had also had considerable experience with seeing human beings in the water. It is the belief of Hobson, Mautin, and others that the sharks became progressively bolder towards humans during the course of the summer. Thus it may be significant that both incidents occurred at the end of the summer.

It appears that one can generalize to this extent. Some species of sharks, for example *C. menisorrah*, are attracted to an area where there are injured fish. Apparently stimuli originating with the injured fish release an excited, highly motivated pattern of exploratory behavior in the shark. At such times many sharks seem to be particularly reactive to any unnatural disturbances created by humans in the general area.

This was illustrated by the response to the commotion at the surface of the water in the first incident. Furthermore, it seems they may also attack a human simply because he is located in an area of high concentration of the postulated stimulating factor, such as occurred in the second incident. In both incidents, visually directed thrusts at the sharks using hands, feet, or spear proved effective in momentarily warding off the attacking shark. Eibl-Eibesfeldt and Hass (1959: 746) and others have also noted the effectiveness of a pointed shaft as a shark deterrent.

CONCLUSIONS

1. Sharks may be expected to appear wherever spear-fishing activities are undertaken, particularly in those areas where aggressive species are known to occur.

2. When sharks appear under these circumstances they may attack a human located within the immediate area of the stimulating factor as well as humans associated with an unnatural amount of activity in the general area.

3. Sharks which have become familiar with the sight of humans in the water may be more likely to attack humans than those which have not.

4. The conclusion reached by others—that visually directed blows, preferably using a pointed instrument (such as a spear shaft), are effective in warding off sharks—is confirmed.

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Pandanus pistillaris in the Caroline Islands: An Example of Long-Range Oceanic Dispersal

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IN CONJUNCTION with the current revision of the genus *Pandanus* (St. John, 1960; St. John and Stone, in sched.) it seems appropriate to mention the factors of dispersal operative in the genus. Since a number of species of *Pandanus* are littoral in habitat, and because at least one (if not several) species is found on nearly every tropical atoll in the Pacific, it has rightly been assumed that oceanic dispersal of the buoyant fruits is responsible for the distribution. There is no question that throughout vast island groups in Micronesia, Melanesia, and Polynesia *Pandanus* has long been part of the indigenous vegetation. There are, in fact, some indications that oceanic dispersal accounts for the farthest limits of the genus, in West Africa at one extreme, Polynesia at the other, the Bonin Islands in the north, and Australia in the south. The actual number of species involved is not yet known, but species of section *Pandanus* (section *Keura* of earlier authors; see St. John, 1960) play a prominent role, especially in the Pacific region. Certain species of other sections of the genus also are primarily ocean-distributed (for example, *Pandanus dubius* Spreng., and *Pandanus tetrodon* (Gaud.) Balf.f.). In general, fruits of these species which are buoyant in seawater exhibit anatomical structures which are presumably adaptations to permit, or prolong, flotation. Brown (1931) has discussed the tissues present in fruits of certain Polynesian species, and uses the apt term aerenchyma to designate the light, pithy, upper mesocarp of such fruits. In addition, the seeds are encased in a highly sclerified osseous endocarp which, except for the minute apertures at either end, are nearly impervious to water. Fruits of this type are capable of remaining afloat for a considerable period. No experiments or observations seem to be available, but it would appear quite probable that a period of 6 months or 1 year in the ocean would not be an exaggerated estimate of the time in which floating fruits could be dispersed by currents.

The vast areas encompassed by some of these species or groups of species with buoyant fruits, and the considerable taxonomic difficulties encountered in the groups, have not heretofore permitted any definite observations to be made with respect to direction of dispersal. Over a period of many years, and because of numerous observations, the knowledge of the currents in the Pacific is now in a position to be of value in problems of oceanic dispersal; but when grave doubt exists as to the nature (and number) of entities involved, little can be said except the obvious, that *Pandanus* species of littoral areas are probably ocean dispersed.

The specimen discussed below, however, because of its unique character, is a reasonably accurate indication of one route of oceanic dispersal. Because it represents a species which is a member of section *Intraobtutus* St. John, it is at once distinguishable from the widely dispersed members of section *Pandanus*.

The specimen was collected by Dr. Ryozo Kanehira, late professor at Kyushu University, Fukuoka, Japan; the label reads, "Mokil Atoll; March 12, 1937, Kanehira no. 4203; nom. vernac. "arowan." Mokil Atoll is an isolated atoll roughly 110 mi. east of Ponape, at 6° 40′ N., 159° 45′ E., consisting of three islands on a circular reef. In April 1957 the present writer visited Mokil, spending the day of the 16th botanizing on the major islet. During this period, 15 numbers of *Pandanus* were collected (all of section *Pandanus*) and many vernacular names

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of plants. The name mentioned by Kanehira "arowan," is a general term used to designate any wild (i.e., nonedible) *Pandanus* or its fruit. The word is apparently of Marshallese origin, where the preferred spelling is "edwaan" (the *d* rolled like an *rr*). The other two islets of Mokil were not seen, so there is no corroborative information regarding the Kanehira collection. There seems no reason, however, to doubt Kanehira's data, and it is assumed that the specimen is indeed from Mokil.

The specimen consists of several phalanges, or keys, of the fruit. The configuration of the carpels which, fused, make up each phalange, determine the section of the genus, and the peculiar "focussed" pattern, as pointed out by St. John (1960) in his discussion of section *Intraobtutus*, is apparent. Although somewhat smaller than Martelli's description and figure indicate, the Kanehira specimen appears to be referable to *Pandanus pistillaris* Martelli. This species, and in fact the section itself, is known only from Melanesia, specifically, from the Bismarck Archipelago. Similar species, and a closely related section (*Lateriobtutus* St. John) occur in New Guinea.

In December 1957 the author observed species of these sections—in particular, *P. pistillaris*—in their native habitats in New Ireland and New Britain. The trees are characteristic of lowland areas, although they may occur at altitudes of 300 m. or more. Frequently they are found along streams, and not uncommonly, near the coast, especially (as near Kavieng, New Ireland) on limestone. Phalanges which had fallen from these trees were occasionally seen as drift along the stream estuaries and along adjacent beaches around Kavieng and northwestern New Ireland. In this area, a considerable variation in fruit size was observed, much more than is indicated by Martelli's description; because of this, and the above factors, the Kanehira specimen, without much hesitation, can be placed as *P. pistillaris*.

If this is established, it is interesting to consider the possibilities for drift. One obstacle is our meagre knowledge of the full, natural range of *P. pistillaris;* there seems, however, to be little question that, if it is not actually endemic in the Bismarck Archipelago, it is restricted to that general area. From a study of the excellent charts provided by Schott (1939) and by Wyrtki (1957), it may be seen that a strip about 5 to 7° north of the equator and east of the 140° meridian, during both seasons of the year, is characterized by a more or less constant eastward flow, which in northern winter emanates from the Mindanao-Morotai region, and in northern summer emanates also from a strong current moving westward and slanting northward along the upper edge of the Melanesian area, but reversing its course in the Mindanao-Morotai region. The northern summer current spans a wider course along the equator, reaching nearly all of the Caroline Islands (except perhaps Palau and Yap) and proceeding possibly beyond the Marshalls. During this season, the route of a drifting object starting from New Britain or in that vicinity would be westward along the northern coast of New Guinea as far as Morotai, thereafter more or less directly eastward through Micronesia. During northern winter, counter currents forming a strong oceanic stream along the northern coast of New Guinea would prevent such a route of drift, while several minor whorl systems in the area bounded by the Admiralty Islands on the west and by the Solomons on the east would make the drift pattern irregular and unpredictable, possibly even somewhat southward. The actual number of miles and the elapsed time at sea must remain a matter of conjecture. No information is available as to the length of time over which floating phalanges may be viable; but indirect evidence (cf. Edmondson, 1941, for data on viability of coconuts after ocean flotation) appears to indicate that distances of 1,000 mi. or more are possible.

Thus it may be seen that the route of drift of an object afloat near the Bismarck Archipelago might, by the devious route outlined, terminate in Mokil Atoll or others of the Caroline Islands. Corroboration of such a route is available. Both Riesenberg (1959) and Sinoto (1960) have reported New Guinea canoe prows washed ashore in the Marshall Islands. Riesenberg (personal communication) has photographs of an entire canoe in the Marshalls which apparently drifted along this same route. Sinoto describes a New Guinea canoe prow which drifted to Nukuoro Atoll.

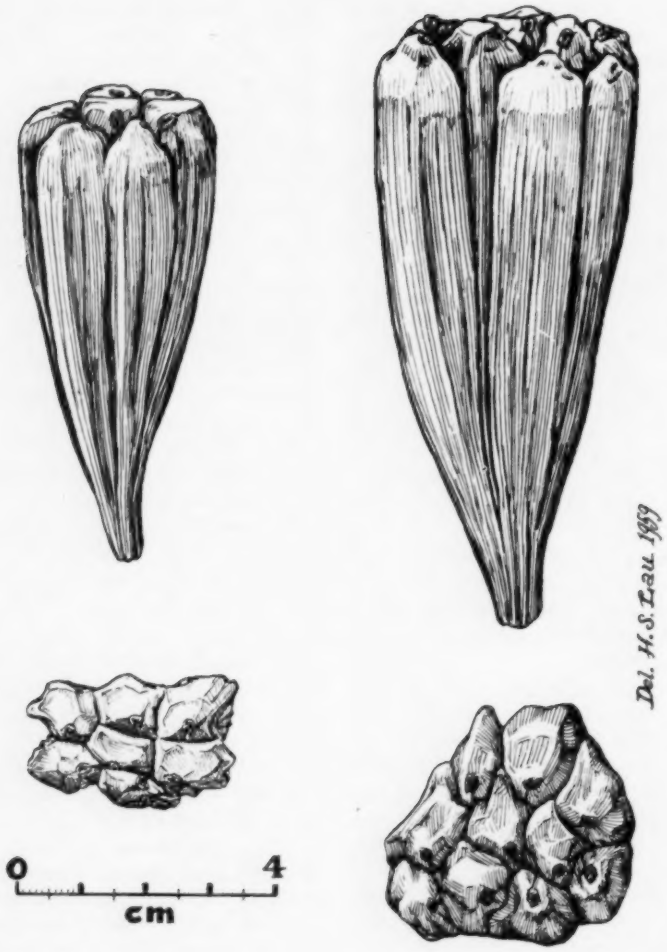

FIG. 1. *Pandanus pistillaris* Martelli. Phalanges in lateral view, natural size, and in top view. Drawn from Kanehira 4203 from Mokil Atoll, Caroline Islands.

It is postulated that the collection of *Pandanus pistillaris* in Mokil Atoll is a further example of such a route of drift. The Kanehira specimens (two of the several phalanges) are here illustrated (Fig. 1).

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